THE BIOLOGY AND SYSTEMATICS OF *FUCHSIA* IN THE SOUTH PACIFIC[1]

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ABSTRACT

There are only four species of *Fuchsia* that are not native to the New World, three occurring on New Zealand and the fourth on Tahiti. The biology and systematics of these taxa are examined here in detail, including known and new information on phenology, habitats, pollination, dispersal, cytology, hybridization, and evolutionary relationships. Because of the basal position of *F. procumbens* in the clade of South Pacific fuchsias and its large suite of unique characters, it is recognized as a new section, *Procumbentes*, within the genus. This leaves *F. cyrtandroides, F. excorticata,* and *F. perscandens* in section *Skinnera*. *Fuchsia* ×*colensoi* is treated here as a widespread and variable hybrid between *F. excorticata* and *F. perscandens*. Keys and descriptions of the taxa are provided.

The genus *Fuchsia* of the family Onagraceae is almost entirely confined to South and Central America. Ranging from Tierra del Fuego north to Mexico, there are nearly 100 species currently recognized in 9 sections (Berry et al., 1988). The occurrence therefore of a group of four species on a few islands of the Southwest Pacific is of considerable phytogeographical interest. Although these species have been treated as comprising the single South Pacific section *Skinnera*, they present a greater diversity of habit than any other section in the genus. The large tree habit in the widespread

F. excorticata (J. R. & G. Forst.) L. f. from New Zealand is found nowhere else in the genus. At the other extreme is the barely woody *F. procumbens* R. Cunningham ex A. Cunningham, a small-leaved and slender-stemmed, decumbent or scandent species that is confined to the far northern coasts of New Zealand. Between these in form is another New Zealand species, *F. perscandens* Cockayne & Allan, a woody liana when mature and found throughout most of the country. The fourth species, *F. cyrtandroides* J. W. Moore, is a small tree and occurs only on the island of Tahiti. All four species have blue pollen, in which they are unique in the genus, and they show a wide diversity in sexual systems, floral and fruit morphology, and seed anatomy.

The last account of the South Pacific species of *Fuchsia* was by Philip A. Munz in 1943. Since then much new information has become available, much of it unpublished, and has prompted a new evaluation of this far-flung outpost of a genus known throughout the world for its horticultural importance.

SYSTEMATIC BACKGROUND AND HISTORY

The kotukutuku of the New Zealand Maori, now known as *Fuchsia excorticata*, was made known to science by Joseph Banks and Daniel Solander, botanists on Captain Cook's first voyage (1768–1771). They first collected it on October 20 and 21, 1769, at Tegadu (now Anaura Bay), which lies to the north of Gisborne on the east coast of the North Island of New Zealand. This was followed by collections at nearby Tolaga Bay, in the north of the North Island at Opuragi (now Mercury Bay), and in the Bay of Islands at Motuaro. It was also gathered at Totaranui in Queen Charlotte Sound in the north of the South Island. These localities are all noted in the unpublished manuscript entitled "Primitiae Florae Novae Zelandiae" (Beginnings of a Flora of New Zealand), which gives detailed descriptions of the plants collected by Banks and Solander. The original manuscript is kept at the Natural History Museum (BM), with a copy at the Landcare Research Herbarium at Lincoln (CHR). In this work, the kotukutuku was placed next to *Epilobium* in the Octandria Monogynia. Instead of recognizing it as a *Fuchsia*, Banks and Solander gave it the new genus name *Agapanthus* (from *agapylos*, pleasant, and *anthos*, flower) and named it *A. calyciflorus* in reference to the prominent calyx lobes. However, this name was never validly published. An attractive color plate showing a leafy shoot with flowers and fruits from Anaura Bay was published by Bea-

glehole (1962) in his edition of the "Endeavour" journal of Joseph Banks, and also by Begg & Begg (1970). The artist was James Miller and the painting was based on a preliminary sketch with notes on the flower color by Sydney Parkinson, one of Cook's artists who died during the return voyage. In the 1980s, color engravings from all the original plates prepared from Captain Cook's first voyage around the world were published for the first time as part of the *Banks' Florilegium* project at the Natural History Museum (BM), and *Fuchsia excorticata* was published as Plate 452 in Part XXII of the series (Banks, 1986).

The kotukutuku was also collected by John Reinhold Forster and his son George, botanists on Cook's second voyage (1772–1775). The locality was almost certainly Queen Charlotte Sound, either between 2 and 25 November 1773, or between 19 October and 10 November 1774, for these were the only times the botanists were on shore during the flowering season. Once again, this plant was not recognized as *Fuchsia*, and Forster & Forster (1776) named their plant *Skinnera excorticata*. The generic name was dedicated to a "percipient, far-seeing" botanist, the Reverend Richard Skinner (1729?–1795), M.A. Oxon, 1753, Rector of Bassingham, Lincolnshire, 1774 (Britten & Boulger, 1931). The specific epithet refers to the peeling bark. The Forsters gave clear drawings of the flower and fruit but curiously interpreted the little petals as nectaries and the berry as a capsule.

The first botanist to classify *Skinnera excorticata* as a *Fuchsia* was the younger Linnaeus (1781), who correctly identified the petals, but also interpreted the sepals and floral tube as part of the corolla. De Candolle (1828) made the first attempt at an infrageneric classification of *Fuchsia*, designating *Skinnera* as one of two sections in the genus; he based this decision on the alternate leaves, ventricose floral tube, and multiseriate ovules of *F. excorticata*.

Plants of the rare, creeping *F. procumbens* were first collected by Richard Cunningham in 1834 at Matauri Bay in northern North Island. He died in 1835 but his manuscript description was published by his brother Allan (Cunningham, 1839). In 1871 Joseph Hooker described a new species, *F. kirkii*, based on plants with larger flowers than those originally described for *F. procumbens*. Just a few years later, however, Hooker realized that the floral size differences were due to sexual dimorphism in the same species, with *F. kirkii* based on the larger male morph and *F. procumbens* based on the smaller female morph (Hooker, 1874).

While preparing his *Handbook of the New Zealand Flora*, Hooker recognized the presence of

fuchsias in New Zealand intermediate in size and habit between *F. excorticata* and *F. procumbens*. He published the species *F. colensoi* for a group of specimens quite variable in leaf size (Hooker, 1867). From one extreme of this variable complex, Cockayne & Allan (1927) described a new lianoid species, *F. perscandens*, from forest remnants near Feilding in the North Island. Their detailed field studies showed it to be distinct from the more variable and shrubby forms attributed to *F. colensoi* by Hooker (1867), Kirk (1899), and Cheeseman (1925). They wrote that the specific epithet indicated "a far more lianoid form than is seen in *F. colensoi*." Thus "perscandens" was not intended to mean "climbing through," as claimed by Moore & Irwin (1978), but "very climbing," in agreement with the usage given by Jackson (1928) that in Latin compounds the prefix "per" increases their force. Allan (1927) also indicated that *F. colensoi* was based on some of the hybrid forms they found to occur frequently between *F. excorticata* and *F. perscandens*.

The last species in this group to be published was *F. cyrtandroides*, described by Moore (1940) from a single individual collected in 1927 from the highest mountain on Tahiti. The specific name is derived from *Cyrtandra* (Gesneriaceae), which has similarly opposite, strongly bicolored leaves in sympatric species such as *C. tahitensis* Nadeaud.

In the only overall treatment of the South Pacific species of *Fuchsia*, Munz (1943) recognized six species, including *F. kirkii* and *F. colensoi*, and placed them all in section *Skinnera*. He was obviously unaware of the sexual dimorphisms present in some of the species, as well as the variability of important morphological traits, for he incorrectly characterized the whole section as having alternate leaves, pendulous flowers, reflexed sepals, and strongly constricted floral tubes.

The present treatment recognizes four species of South Pacific *Fuchsia*. Three species remain in section *Skinnera*, also the common and variable hybrid entity, *F. ×colensoi*. However, a new section, *Procumbentes*, is proposed herein for *F. procumbens*, based on a series of fundamental differences from the other South Pacific species.

Habit and Deciduousness

The first resident botanist in New Zealand to describe the adult plant of *Fuchsia excorticata* was Thomas Kirk in his classical works, *The Forest Flora of New Zealand* (1889) and the unfinished *Students' Flora of New Zealand* (1899). In the former he wrote, "It is of irregular growth, varying from a much-branched shrub to a small tree 45 ft high, with a short trunk often gnarled, from 1 ft to 3 ft in diameter, and thin bark of a bright reddish-brown hue, which on old specimens divides into numerous paper-like flakes of layers."

This maximum height of *F. excorticata* was reported as 40 ft. by Cheeseman (1906, 1925), later converted to 12 m by Cockayne (1921, 1928) and Allan (1961). A tree of this size is shown in Figure 1, but such veterans are rare. It is now difficult to find trees taller than 9 m, at which height the crowns can be small in relation to the trunk and are often enveloped by lianas. When in the forest, the trunk can be single and well developed (Fig. 2), and is either erect or can slope toward the light above a stream, or even lie prostrate for 3–4 m until the streamside is reached, where it grows upwards. In more open situations, such as induced shrubland or along roadsides, the main trunk is less than 1 m tall and divides into several secondary trunks to form a large shrub up to 4 m high. Branching is erect (fastigiate; Kirk, 1899), and the growth of twigs is sympodial. Bussell (1968a) stated that the tips of *F. excorticata* shoots "shrivel and abort" at the end of the growing season and that growth is continued by the most distal remaining lateral bud. Christensen (1923) noted that branches of *F. excorticata*, partially buried by shingle rocks on the bed of the Perceval River near Hanmer, "had put forth numerous roots from 1 ft to 3 ft in length."

The wood anatomy of *F. excorticata* has been described by Meylan & Butterfield (1978) and Carlquist (1977). It can be considered quite mesomorphic, although the inner wood has shorter, narrower, and denser vessel elements than the outer wood. Growth rings are not evident in either the inner or outer wood, and starch is stored in the libriform fibers (Butterfield & Meylan, 1973). The wood is suitable for small cabinetry items and can be worked on a lathe to produce fine bowls and similar items. Contrary to Carlquist's report, crystals are present in the wood (R. Patel, pers. comm.). Twigs snap easily, but Kirk (1889) noted that "the wood is extremely difficult of combustion, and like the rewarewa (*Knightia excelsa* R. Br.) is often termed 'bucket of water wood' by the bushmen; even when thoroughly dry it can scarcely be burned in an open grate." The periderm in *Fuchsia excorticata* arises beneath the phloem sclerenchyma, and there is an extensive phelloderm layer (Robinson & Grigor, 1963).

Fuchsia excorticata stands out as one of the few deciduous trees indigenous to New Zealand. Russell (1936) described the mechanism of leaf abscission and found that leaf fall in Dunedin (46°S)
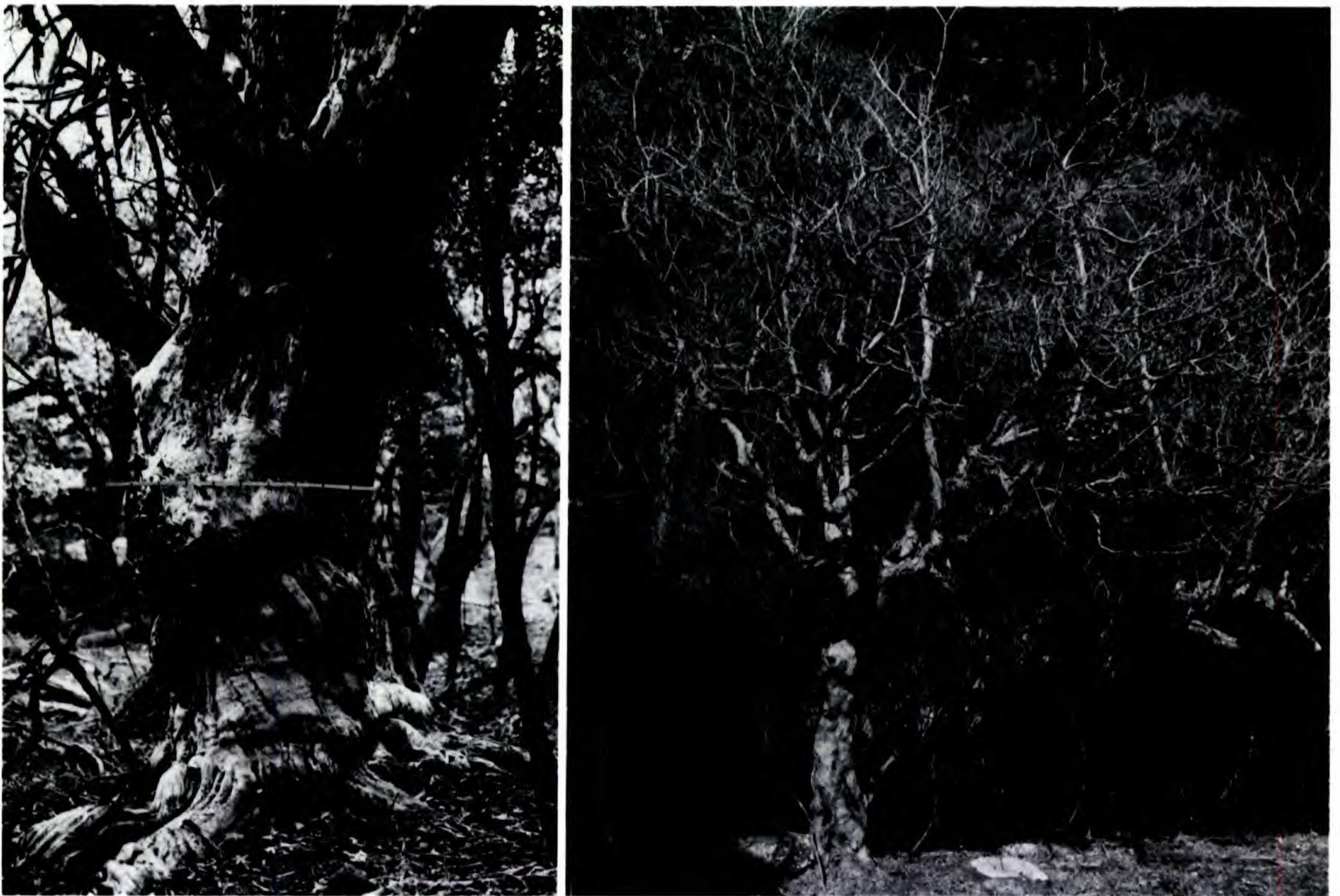
FIGURES 1, 2.—1 (left). A veteran tree of *Fuchsia excorticata* at Hinewai, Banks Peninsula, South Island, New Zealand. Overall height ca. 12 m; height to first branches 2.25 m; circumference (breast height) 2.5 m. Photograph by M. Oelderink.—2 (right). A leafless tree of *Fuchsia excorticata*, shortly before leafing out. Height of main trunk is 1.8 m, diameter at breast height is 28 cm. Kaituna Valley, Banks Peninsula, South Island, New Zealand, 6 September 1988. Photograph by E. J. Godley.

began during early May in 1934 and was complete within 3 to 4 weeks. The trees remained leafless during most of June, all of July, and early August, with new leaves appearing by the middle of August. Bussell (1968a, b) reported that leaf fall in Dunedin occurred throughout the growing season, with two distinct peaks, one in midsummer and the other in autumn. Bud break on marked shoots of *F. excorticata* began about 1 September in 1963 and on 20 August in 1964 (mean August and September temperatures in Dunedin were 1.5°C lower in 1963). This and other evidence led to the conclusion that the start of the growing season is controlled mainly by temperature. On the Port Hills near Christchurch (43°32′S), Suckling (1914) noted that leaves "are lost in May and appear in August."

In the North Island, the Auckland botanist Crookes (1926) stated that *F. excorticata* is "only deciduous in *mountain* districts of the North, but is regularly deciduous in the South" [italics ours]. Moore & Irwin (1978) stated that the leaves last through winter in the north. However, A. E. Esler (pers. comm., 25 Aug. 1980) noted a mixed pattern of leaf fall in local populations in Auckland

(36°52′S) during the relatively mild winter of 1980—all mature bushes were completely deciduous, although young growth on stems up to 2 cm diameter and juvenile plants perhaps 2 to 3 years old retained their leaves.

In *Fuchsia cyrtandroides*, mature individuals range from strongly branched shrubs 2–3 m tall in exposed situations (Fig. 3) to small trees 5–6 m tall with irregular trunks and a stem diameter of 20 cm in small, more protected valleys. The bark is brown and smooth on young stems, not obviously peeling off the trunk as in *F. excorticata*. Carlquist (1975, 1977) presented some data on wood anatomy of *F. cyrtandroides*, indicating it to be highly mesomorphic for the family, with few, wide vessel elements. He suggested some seasonality in flowering and leaf production in this species when he stated that he had "seen *F. cyrtandroides* on Tahiti during July, the dry season, flowering on branches that are virtually leafless" (Carlquist, 1975). All trees observed in September 1973 by E. Godley were in full leaf and flower, and trees observed in February 1988 by P. Berry were all in full leaf, but flowers were extremely scarce.

FIGURE 3. Shrubby habit of *Fuchsia cyrtandroides* on an exposed ridge, Mont Marau, Tahiti. Photograph by P. Berry.

The adult of what is now called *Fuchsia perscandens* was described by Cockayne (1912) as "a shrub in the open and at times a scrambling liane in the forest." Bird (1916) traced the development of these growth forms (under the name *F. colensoi*) in Riccarton Bush, Christchurch. The primary shoot generally grows up to 35 cm high without support and then follows one of three pathways. It can push up between the branches of a shrub and search for further support on emergence, or it can trail along the ground for 1–2 m, rooting and giving off lateral branches, one or more of which may find support. If no support is found, the stems may form prostrate or cushion-like masses up to 1 m high on the forest floor.

Shrubs in the open can apparently originate either from nonsupported plants that developed within a forest which was later opened up, or from plants which developed outside forest where no support was available. In exposed situations, the search for support is greatly impeded because shoots that protrude from the surface of the shrub are usually killed back by cold or dessication, and growth arises from lateral buds further back, as in *F. excorticata*. The extent and size of the lianoid form can best be seen in forest remnants where the support has collapsed and the cable-like stems, up

to 6–7 cm in diameter, lie near the ground (Fig. 4). Plants cultivated without support usually adopt the open bushy habit of this species.

Bird (1916) noted that in Riccarton Bush, near Christchurch, "Plants in exposed situations lose their leaves early in winter, but in the shade they are devoid of leaves for only a few weeks." On roadside plants of *F. perscandens* in a bush remnant at the Sign of the Bellbird, Port Hills, Christchurch, E. Godley noted that on 5 May 1988 there were many dead leaves, perhaps due to a recent frost. On 10 June 1989, there were occasional leaves, but by 11 July all plants were leafless. In 1987, 1988, and 1989, leaves had appeared by the first week of October.

In contrast to Christchurch, a specimen of *F. perscandens* collected from the coastal lowlands at 39°56'S in North Island was in full leaf in July 1970 (Wanganui East, CHR 209534). Further inland and a little further south, specimens from several localities near Feilding showed new leaf flushes from early September to mid October.

Natural populations of *Fuchsia procumbens*, although confined to the warmer north of New Zealand, are nearly or completely deciduous in winter, when the bare slender stems are only made conspicuous by the red fruit. Even as early as 21 Jan-

FIGURE 4. Lianoid habit of *Fuchsia perscandens* in a forest remnant, North Canterbury, South Island, New Zealand. Diameter of the stem is 6.25 cm. Photograph by F. Allan.

uary, plants bare of leaf but full of berries have been recorded (Godley and Reynolds, pers. obs.). On the other hand, a plant cultivated at Akaroa, South Island (43°49′S), was evergreen. Thomson (1909) recorded that plants cultivated outdoors in Dunedin were killed during an exceptionally cold spell in July.

HABITAT

Fuchsia excorticata. This is the most widely distributed and common of the South Pacific species of *Fuchsia*, with a range from ca. 34°S near the North Cape of New Zealand to ca. 50°33′S on Auckland Island. Cockayne (1910) wrote, "There is hardly a forest in New Zealand where the native fuchsia, the kotukutuku of the Maoris, may not be seen." In his descriptions of New Zealand vegetation, Cockayne (1921) mentioned this species in North Island habitats as diverse as *Corynocarpus* coastal forest on the Wellington coast or Kapiti Island and *Libocedrus bidwillii* Hook. f.–*Podocarpus hallii* Kirk subalpine forest of Hauhangatahi (780–1140 m) and Mount Egmont (above 850 m). In South Island, the habitats include *Hebe elliptica* (Forster f.) Pennell coastal scrub at the base of Bluff Hill and *Podocarpus totara* D. Don forest on Banks Peninsula. Cockayne also mentioned *F. ex-*

corticata as one of the principal species of small tree associations near riverbanks and as an invader after retreat of glaciers and after forest has been milled and burned.

At present, however, *F. excorticata* is quite uncommon in many areas, even though forest remnants or secondary shrubland are still present. Much research has shown that browsing by the introduced bushtail opossum (*Trichosurus vulpecula* Kerr) can play an important part in the death of *F. excorticata.* In 1946 and 1947 in the Orongorongo Valley, North Island, *F. excorticata* was the main opossum food in the lowland broadleaf-podocarp forest (Mason, 1958). Almost 30 years later, Fitzgerald (1976) noted that *Fuchsia excorticata* was no longer abundant anywhere in the 93-ha forest, and the few large plants remaining and their seedlings were constantly being browsed by opossums and other browsing animals. In the upper Waiho Valley, South Westland, South Island, Fitzgerald & Wardle (1979) noted serious damage to *F. excorticata* involving death or defoliation, whereas on the roadsides and forest margins in the lower part of the valley plants remained vigorous despite browsing. On Banks Peninsula, eastern South Island, *F. excorticata* was the plant food favored by the opossums (Gilmore, 1967). Despite this, *F. excorticata*

is still one of the most common roadside trees or shrubs on the peninsula, possibly because white clover and grasses are also important opossum foods in this predominantly pastoral area.

On Stewart Island, Wilson (1987) found the ko-tukutuku to be rather local but scattered throughout the island, having been reduced mainly by opossums. He noted that on certain inland sites, *Fuchsia* was probably never prominent, even before the introduction of browsing mammals, apparently due to low soil fertility.

A significant feature in the distribution of this species, considering the many-seeded edible fruit, is that it is poorly represented on the offshore and shelf islands. In the north, *F. excorticata* has not been recorded from Three Kings and Poor Knights Islands. It is found, however, on the Hen and Chicken Islands and on the two largest northern offshore islands, Little Barrier and Great Barrier. In the Bay of Plenty, it is not recorded from Mayor Island. In the south, it has been recorded only relatively recently on the two largest shelf islands. It was first gathered on the Chatham Islands in 1957 by Madden, who wrote about it, "Now spreading within the small area of Maipito Flats near Waitangi. Deliberately planted below the house many years ago by a nostalgic housewife" (Madden & Healy, 1959). The only collections since then have come from the same locality, Maipito to Lake Huro. In 1976, when visiting the island, G. Hamel (pers. comm.) was assured that *F. excorticata* was introduced there "about 90 years ago."

On the far southern Auckland Island, *F. excorticata* has also been found at only one locality. This population lies at the head of Laurie Harbour in the Ross Harbour area at the north of the island (ca. 50°33′S) and was found by B. C. Aston on 7–8 January 1909 (Cheeseman, 1909, appendix). Godley (1985) recorded that on 30 December 1962, he saw four trees near the mouth of the Grey Duck Stream, all with trunks 35–45 cm DBH. All were in flower and were hermaphroditic. These were the only trees seen while wading down the stream to its mouth, after descending to the valley from north of Cloudy Peak. In early April 1980, C. D. Meurk (1982) saw *F. excorticata* "scattered along a small tributary (from ca. 75 m elev.) entering south side of Grey Duck Creek ca. 200 m from the mouth, and down to sea level at the head of Laurie Harbour—in association with the rare *Asplenium bulbiferum* Forst. f." Just as the populations of *Olearia colensoi* Hook. f. var. *grandis* Simpson around Ross Harbour arose from a relatively recent introduction (Godley, 1965), so could this population of *F. excorticata*. But whereas the *Olearia* populations are definitely

associated with the activity of man, *Fuchsia* apparently is not.

Fuchsia cyrtandroides. The interior of the island of Tahiti (ca. 17°32′S) is mountainous with an estimated rainfall of 3000 mm for Mt. Marau, and 5000 mm for Mt. Orofena (J. Florence, pers. comm.). Precipitous ridges lead to the central peaks, and tracks follow the ridges. It is along these tracks that *F. cyrtandroides* has mainly been found, although not in abundance (Fig. 5). Godley (1983) reported finding 11 trees on the Marau ridge at about 1400 m, and three trees high up the Aorai trail; he also noted that in the more temperate climate of these higher altitudes, the fuchsia grows in association with several other genera found in New Zealand, e.g., on Aorai: *Astelia, Blechnum, Cyathodes, Freycinetia, Gleichenia, Metrosideros,* and *Weinmannia*. Associated taxa observed by Berry in 1988 on the Marau ridge were *Cyathea* spp., *Cyrtandra tahitensis* Nadeaud, *Coprosma, Freycinetia, Metrosideros, Myrsine, Scaevola tahitensis* Carlquist, *Sclerotheca jayorum* J. Raynal, *Streblus, Vaccinium,* and *Weinmannia parviflora* Forst. f.

As for habitats other than ridge tops, M. van Balgooy, who visited Tahiti in September 1971, reported in a letter to P. Raven that *F. cyrtandroides* is much more common in the deep shaded valleys than along the ridges, where most of the paths are located. He considered it to be one of most common members of the montane forest between 1400 and 2000 m. In a letter to P. Raven in August 1969, F. R. Fosberg recalled that his 1934 collection of *F. cyrtandroides* was in one of the wettest, mossiest forests he had ever seen, with abundant tree ferns and fronds of *Asplenium nidus* L. up to eight feet long.

In 1983, a cyclone toppled and severely altered the tall cloud forest, which is now much more open; in February 1988, all trees seen by P. Berry on the Marau ridge were heavily affected by gall midges (Cecidomyiidae), whose larvae cause galls on leaves.

Fuchsia perscandens. The distribution given by Allan (1961) from 42°S in South Island to 40°14′S in North Island (forest remnant near Feilding) should be extended to 37°18′ to 46°36′S (Fig. 6). The northernmost record (as *F. colensoi*) was made by Cheeseman in January 1875, from somewhere in the Northern Wairoa (AK). All that we know is that during this "hurried examination" of the district, Cheeseman collected *Juncus tenuis* Willd. in the upper reaches of the Northern Wairoa River near Omana (35°54′S) and that he went higher up and lower down the river (Cheeseman, 1879). He
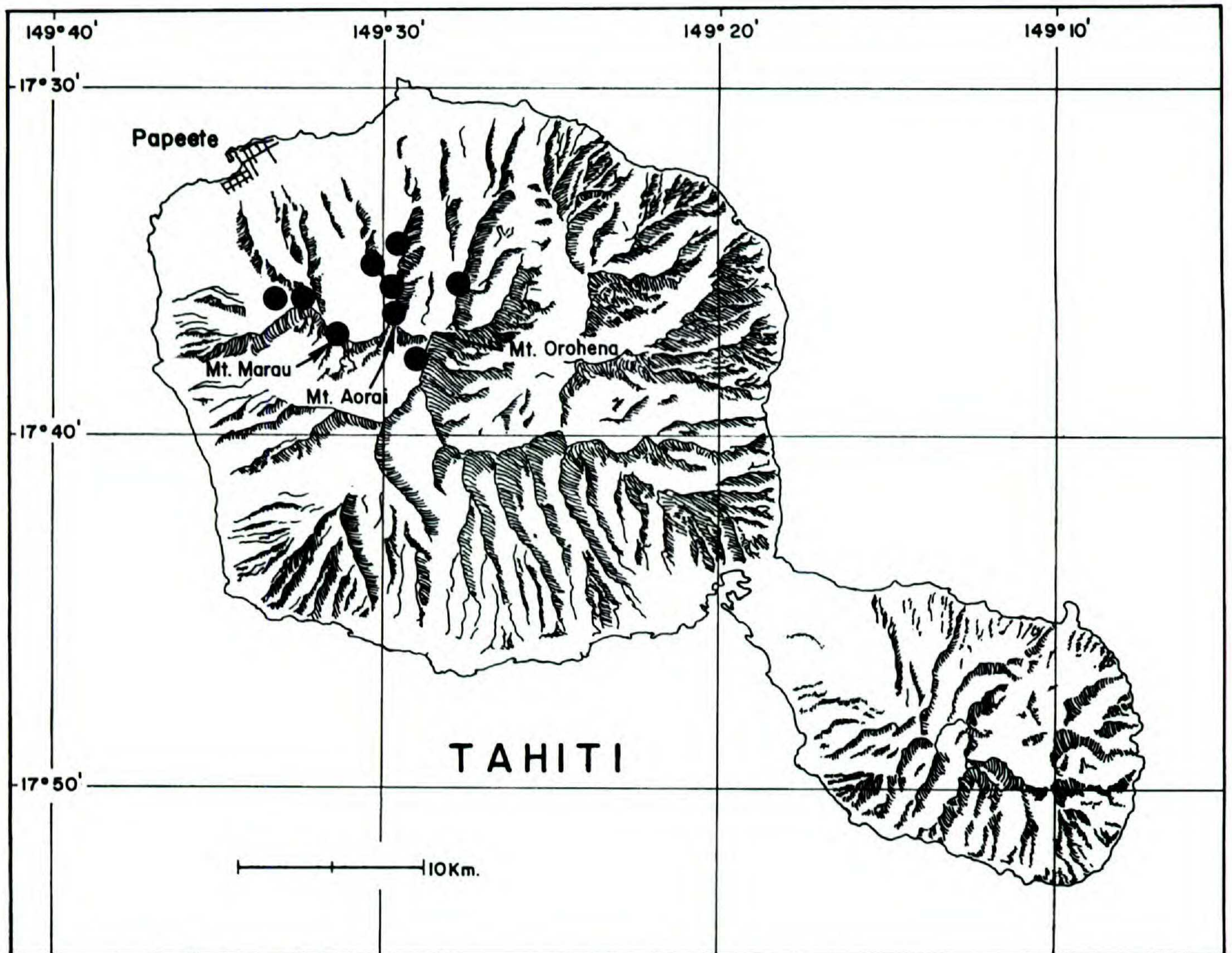
FIGURE 5. Native distribution of *Fuchsia cyrtandroides*. Drawing by E. Pérez.

may have approached the district from Whangarei. This is the only record of *F. perscandens* north of Auckland, and the population is probably now extinct due to forest clearing.

From just south of Auckland, in the lower Waikato, there are two other early records. In 1870 Kirk gathered specimens (WELT) from forest adjacent to Lake Whangape (37°28′S), noting, "A *Fuchsia*, of sub-scandent rambling habit, was found here, but without flower or fruit; it is perhaps a form of *F. colensoi*" (Kirk, 1871); and at nearby Opuatia Creek he found a "*Fuchsia* sp. in habit resembling *Muehlenbeckia adpressa*, no flower or fruit" (WELT). Both collections are *F. perscandens*, and their populations are probably extinct.

The northernmost localities known at present are at 37°15′S in swamp forest of *Dacrycarpus dacrydioides* (A. Rich.) de Laubenf. (white pine) and *Laurelia novaezelandiae* A. Cunn. near the Kopuku Coal Mine, where the species was locally common around tree bases in 1980 (CHR), and to the east at 37°18′S in derelict *D. dacrydioides* forest 12 km NW of Paeroa, where very few plants were left in

1980 (CHR). These are "relict populations of a probably abundant plant of the once very extensive lowland white pine forests in the lower Waikato area" (Bartlett, 1984).

At Te Aroha, in the Thames Valley, 20 km south of Paeroa, Cheeseman collected *F. perscandens* in 1884 (AK). But south of the lower Waikato and the Thames Valley, in the middle Waikato basin, *F. perscandens* continues to be rare. It was not listed by M. C. Gudex in his several reports on forest remnants, and *F. ×colensoi* was reported as rare (Gudex, 1963). In 1991, a single female plant was found in Hammond Bush, Hamilton (37°38′30″S) (CHR). The species is not recorded again until near Te Koraha (38°13′S) west of Otorohanga (AK). Further to the east, *F. perscandens* almost reaches the coast at Whakatane (37°58′S), Bay of Plenty (AK), again in a remnant of white pine forest; and in the far east of North Island it reaches ca. 38°33′S, 16 km north of Gisborne, where it was sprawling down a grassy bank (Cresswell, 1976).

Southwards, *F. perscandens* is found throughout both North and South Islands but is not common.
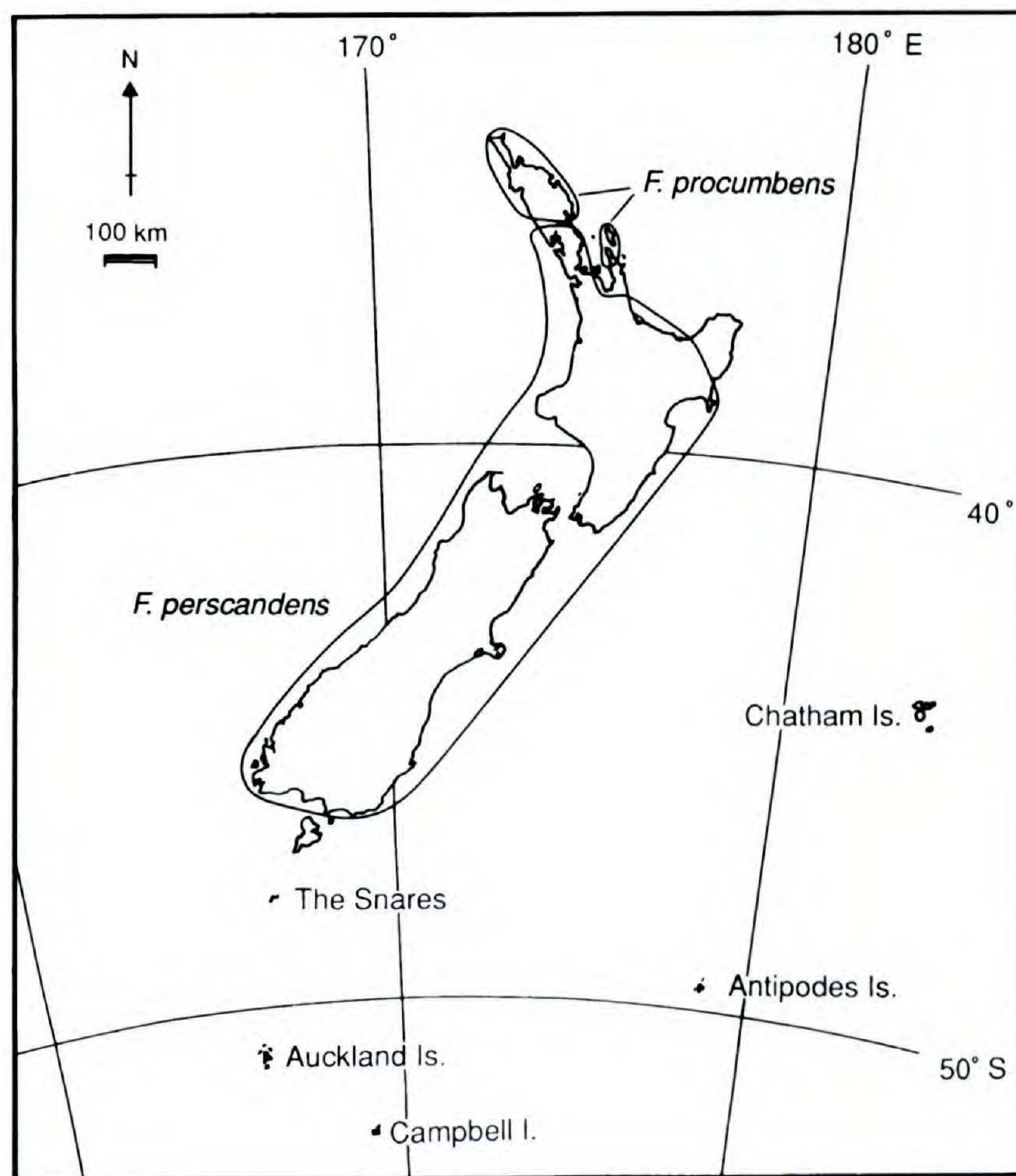
FIGURE 6. Native distribution of *Fuchsia perscandens* and *F. procumbens*, in New Zealand. There is currently no overlap in the distribution of these two species, with *F. procumbens* restricted to the northern part of the North Island. *Fuchsia excorticata* is widespread in New Zealand, occurring throughout the North and South Islands, as well as on Stewart Island (shown between The Snares and the southern tip of the South Island on the map), Chatham Island, and Auckland Island. Drawing by S. Malcolm.

It is recorded from coastal rocks and wind-shorn coastal scrub, in Westland, South Island; the highest altitudes are 1700–1800 ft. (518–549 m) north of Taihape in central North Island and 1500 ft. (457 m) on the Hunters Hills, eastern South Island. Common habitats are river terraces and remnants of white pine swamp forest, but it is also recorded from limestone in the Wairarapa (North Island) and Marlborough (South Island). The southernmost record is from coastal scrub at Bluff (46°36'S) on the shores of Foveaux Strait.

Fuchsia procumbens. This species is confined to the coastal regions of northern New Zealand in lower latitudes than *F. perscandens* (Fig. 6). The northernmost record is from Kerr Point (34°24'S) near North Cape. Southwards, *F. procumbens* reaches Maunganui Bluff (35°46'S) on the west coast of North Auckland, and Bream Head (35°51'S) on the east. It then reappears further east on Great Barrier Island, from where it extends south to Kennedy Bay (36°41'S) on the Coromandel Peninsula. It is not recorded from any of the many islands around the

North Auckland and Coromandel coasts, except the largest, Great Barrier.

Since its discovery in 1834, *F. procumbens* has been recorded from 51 localities (38 in North Auckland; 6 on Great Barrier; 7 on Coromandel), and at several of these there is more than one population. From 1834 to 1901, only 15 localities were recorded, and Cheeseman (1906) understandably described *F. procumbens* as "rare and local." This impression was reinforced when only five new localities were added from 1907 to 1945. But since 1946, 31 more localities have been discovered, several the result of boat surveys of coasts otherwise difficult to reach (Godley and Reynolds, unpublished manuscript).

Despite its limited latitudinal and altitudinal range, *F. procumbens* occupies a diversity of habitats. Although not a true psammophyte, it grew at Matauri Bay on "the sands immediately above the range of the tide" (Cunningham, 1839), and Cheeseman (1897) found *Ipomoea palmata* Forssk. and *F. procumbens* "plentiful along the beach" south of North Cape. It is likely that these were old

foredunes, relatively stable, and with damp places for the *Fuchsia.*

On the northeast coast of Great Barrier Island, Wright & Cameron (1985) noted *F. procumbens* in a unique low herb field at four stream mouths. The associated species included *Arthropodium candidum* Raoul and *Leptinella dioica* Hook. f., reaching their northernmost distribution here, with *Ophioglossum petiolatum* Hook. forming the only large, secure population of this fern known in New Zealand. On sheltered rocky or shingle foreshores, where sandy beaches do not intervene, or on the margins of mud flats, *F. procumbens* can grow to within 2–3 m of the high tide mark. Here it can scramble among the irregular bases of the trunks of the pohutukawa, *Metrosideros excelsa* Soland. ex Gaertn. (Myrtaceae), a common coastal tree of northern New Zealand, or form carpets in the open. Further back from the coast, *F. procumbens* can be common on the floor of pohutukawa forest (particularly where light has been let in), where it scrambles through the sward of the grass *Microlaena stipoides* (Labill.) R. Br. or patches of the aggressive adventives *Stenotaphrum secundatum* (Walter) Kuntze and *Pennisetum clandestinum* Hochst. ex Chiov. (kikuyu grass). Most woody species do not provide a suitable support for *F. procumbens.* An exception is the small shrub *Coprosma rhamnoides* Cunn., through whose dense divaricating branches *F. procumbens* scrambles to nearly 1 m above the ground.

Fuchsia procumbens is also regularly associated with two other native species, the flax, *Phormium tenax* Forster & G. Forster, and a cutty grass, *Cyperus ustulatus* A. Rich. It scrambles through flax clumps on the margins of streamlets (often summer-dry) in pohutukawa forest, or on steep open slopes above beaches; and it scrambles through the cutty grass in damp dune hollows (see above) or on old, dry, well-drained shingle beaches, or in local swampy patches. In disturbed areas, remnants of flax can provide a refuge for *F. procumbens.*

The highest altitude recorded for *F. procumbens* is on the precipitous coasts of the Cape Brett Peninsula. Here, the land mass rises steeply from the shore, and *F. procumbens* is found from near sea level to ca. 150 m elevation in a variety of situations—dry forest floor, moist stream sides, full sun and deep shade, gravelly soil, and dry clay.

Except for such a major change as roadmaking, human activity has not had obvious deleterious effects on populations of *F. procumbens.* It can be found draped over old fences or twining through the introduced blackberry (*Rubus fruticosus* L.). Long-term observations show that if already estab-lished, it keeps pace with the growth of buffalo grass and kikuyu and is not overwhelmed. Cattle do not appear to eat *F. procumbens.* However, trampling can bare the ground, leaving remnant patches of *F. procumbens* round the bases of trees or under fallen trunks. In reserves where cattle have been removed, *F. procumbens* is now flourishing. In such circumstances it seems highly probable that re-expansion is due to the scrambling and rooting habit of *F. procumbens.* Certainly this habit is very successful in maintaining unisexual populations, for example, an isolated female population on the Coromandel coast, first observed in 1929, was still present in 1990.

Fuchsia procumbens can still be described as local, but it is not as rare as described by Cheeseman (1906, 1925), and is not endangered as listed by Given (1981). It is also often grown in gardens. Only a few examples of local extinction are known, and the population with the longest known history (Mine Bay, Great Barrier Island) has existed from at least 1867 to 1989. Although recorded from several reserves, protection is not necessarily guaranteed there, particularly if the reserve is for recreation and frequented for swimming and picnics. Rather, *F. procumbens* is best protected by growing in relatively inaccessible places, or, if accessible, by its inconspicuousness and its similarity to the common twiner, *Muehlenbeckia complexa* Meissn.

FLOWERING TIMES

Fuchsia excorticata. The flowering time of August to December (late winter to early summer) given by Cheeseman (1906, 1925) and copied by Allan (1961) covers the period when plants will almost certainly be in flower in the lowlands. But it is not unusual for flowering to begin in June to July (early to mid winter) and to extend into January (mid summer), as shown by the following field notes made by E. Godley. On 10 June 1981, two out of four marked trees in the Kaituna Valley, Banks Peninsula, had scattered flowers. On 15 June 1977 at Gillespies Beach, Westland, several trees had flower buds, flowers, and green fruits; on 29 June 1980, at the Sign of the Bellbird, Christchurch, all four marked trees had flower buds, and one had open flowers. Cameron (1991) observed that on 3 July 1991 in Kauri Park, Auckland, plants of *F. excorticata* had many flower buds and flowers ranging from young to mature or shed, and Jones (1990) observed many flower buds and flowers on 14 July 1990 in Titirangi, Auckland. On Banks Peninsula, E. Godley found some trees still in flower on a plateau above Pigeon Bay on 21
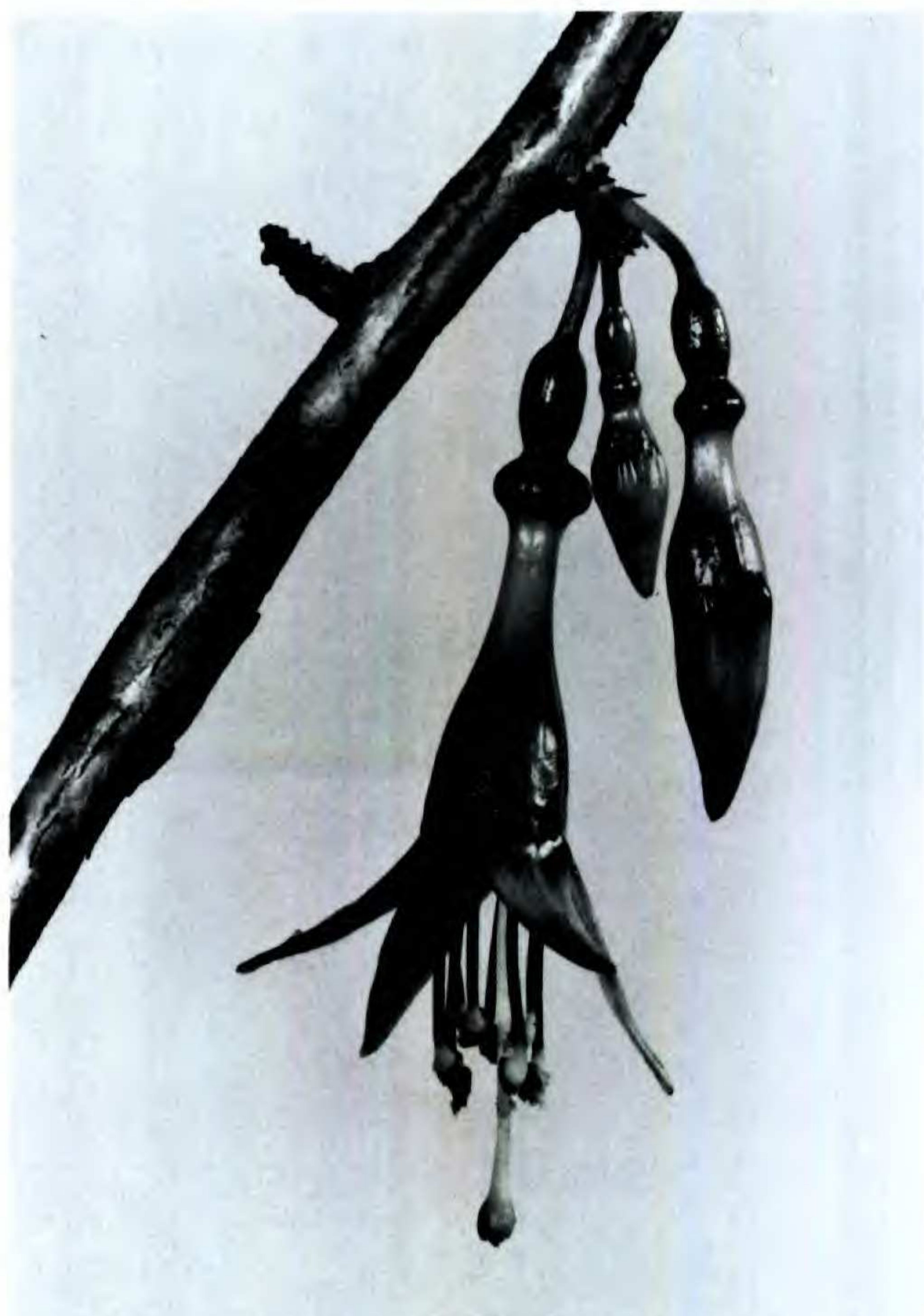
FIGURE 7. Ramiflory in *Fuchsia excorticata*. Photograph by R. Lamberts.

January 1989, at ca. 500 m elevation, but on 24 January of the same year, there were no flowers remaining on four marked trees in the Kaituna Valley.

Individual trees also have a long flowering period. The first flowers are produced on the older branches or on the trunk; they appear when the trees are leafless and mature in acropetal succession on leafless condensed shoots (Fig. 7). The second wave of flowers is borne on leafy shoots produced from the youngest twigs; the flowers are solitary in the axil of each leaf and mature from the base to the tip of the twig. Both axillary and ramiflorous flowering continue to the end of the flowering period. For an hermaphroditic tree grown from seed from Kaituna Valley and cultivated at Lincoln, outside Christchurch, the flowering period lasted 145 days in 1989, with the following sequence: ramiflory only from 23 July to 22 September (61 days), then both ramiflory and axillary flowers from 23 September to 4 December (84 days). In the 1992 to 1993 flowering season, the same plant flowered for 130 days, ramiflorous only from 31 August until 16 October (47 days), then ramiflorous and axillary together from 17 October to 8 January (83 days).

An unusual situation was noted on Banks Pen-

insula involving a tree near Duvauchelle on a shaded southern aspect, and another at Pigeon Bay 2 km away with a more sunny northern aspect. When first seen on 31 March 1991 (early autumn), both bore flower buds, flowers, and fruits; and these three stages were present at approximately monthly intervals (although in varying amounts) until 18 December, a period of 262 days. There was then a gap from January to March 1992, when flowering began again.

The few observations at higher altitudes show a much shorter flowering period, mainly due to a later start. At the Maruia Springs Hotel (650 m elevation), in the north-central part of the South Island, three marked trees (two female, one hermaphrodite) were observed by E. Godley in late 1981 to early 1982 as follows: on 14 October, leaf buds were just beginning to open, and flower buds were up to 5 mm long and very sparsely scattered over the branches. By 26 December, the plants were in full leaf, with occasional flower buds and flowers at all stages of development, with green fruits present. By 8 January, plants were in full leaf, but two of the three plants had just finished flowering, and one female still had scattered flowers. An estimate of the flowering period there would be from 1 November to 12 January (73 days).

Fuchsia cyrtandroides. There appears to be some flowering seasonality in this species, based on the few observations available, with flowering concentrated in the drier part of the year. On Tahiti in September 1971, M. van Balgooy saw hundreds of plants of *F. cyrtandroides*, "Nearly all abundantly fruiting and some still flowering. . . apparently the flowering season is around July–September" (pers. comm. to P. Raven). Sherwin Carlquist observed *F. cyrtandroides* in June 1962 and commented, "The plants were flowering on virtually bare branches, a habit that suggests marked seasonality in flowering" (pers. comm. to P. Raven). In September 1973, all 11 plants seen by E. Godley on Mt. Marau were in flower, as well as the three plants seen on the Aorai trail. Paul Berry visited Mt. Marau in early February 1988, and out of about 25 small trees that were checked, only one individual was still in flower. This same tree had a few fleshy berries, while only two other trees had fruits remaining on the tree, and these were completely dried out.

Fuchsia perscandens. Flowers are produced, usually singly, from either the bare stems, or from the short stems of the leafy shoots. Allan (1961) gives a flowering time of September to October, but flowering specimens in CHR range from 20 August at Makino, near Feilding, to 25 March at Boundary

Creek, Rangitata River. In between these dates, the greatest number of flowering individuals were collected in October (14 specimens) and November (7 specimens).

Fuchsia procumbens. Flowers are produced singly in the leaf axils. Allan's (1961) flowering time of December to February can be extended from October to April. A continuous female sward at Kennedy Bay, Coromandel Peninsula, (possibly a single plant) was in full flower on 13 October 1990 and still had a few flowers and flower buds on 16 February 1991. These 126 days suggest a flowering time of 140 to 160 days. April flowering is recorded from Matauri Bay and Whangaruru in North Auckland (Godley and Reynolds, unpublished obs.).

FLOWERS AND BREEDING SYSTEMS

Fuchsia excorticata. Thomson (1881) recognized "two very distinct forms of flowers" in this species. The larger form was hermaphrodite and protogynous, and the smaller female. However, Kirk (1889) considered the flowers trimorphic, "the differences depending chiefly on the relative length of the stamens and style"; he also noted that his long-styled flower was female, and that his mid- and short-styled flowers were hermaphroditic. Later, Kirk (1893) related the situation in *F. excorticata* to the heterostyled trimorphic species studied by Darwin (1877). However, he added in a footnote, "If it were not for the two forms of hermaphroditic flowers, the New Zealand fuchsias might be termed gynodioecious." Kirk's classification was widely accepted until Godley (1955) showed that the situation in *F. excorticata* had nothing to do with true heterostyly. The division of hermaphroditic plants into "short-" and "mid-styled" forms could not be upheld, particularly as both types could be found on the same tree. The species is in fact gynodioecious (Fig. 8), with hermaphrodite plants self-fertile. In 12 natural populations the percentage of female plants averaged 26.9% (total of 1394 plants, with a range of 4.1% to 40.4% females).

Fuchsia perscandens. Allan (1927) also used the terminology of Kirk, but this species is again gynodioecious, with flowers that are smaller copies of *F. excorticata* (Godley, 1955). Twenty-six flowering individuals grown at CHR comprised 19 hermaphrodites and 7 females.

Fuchsia cyrtandroides. This species is hermaphroditic. As in *F. excorticata* and *F. perscandens,* the relative lengths of stamens and style (and hence stylar protrusion) can vary on the same plant
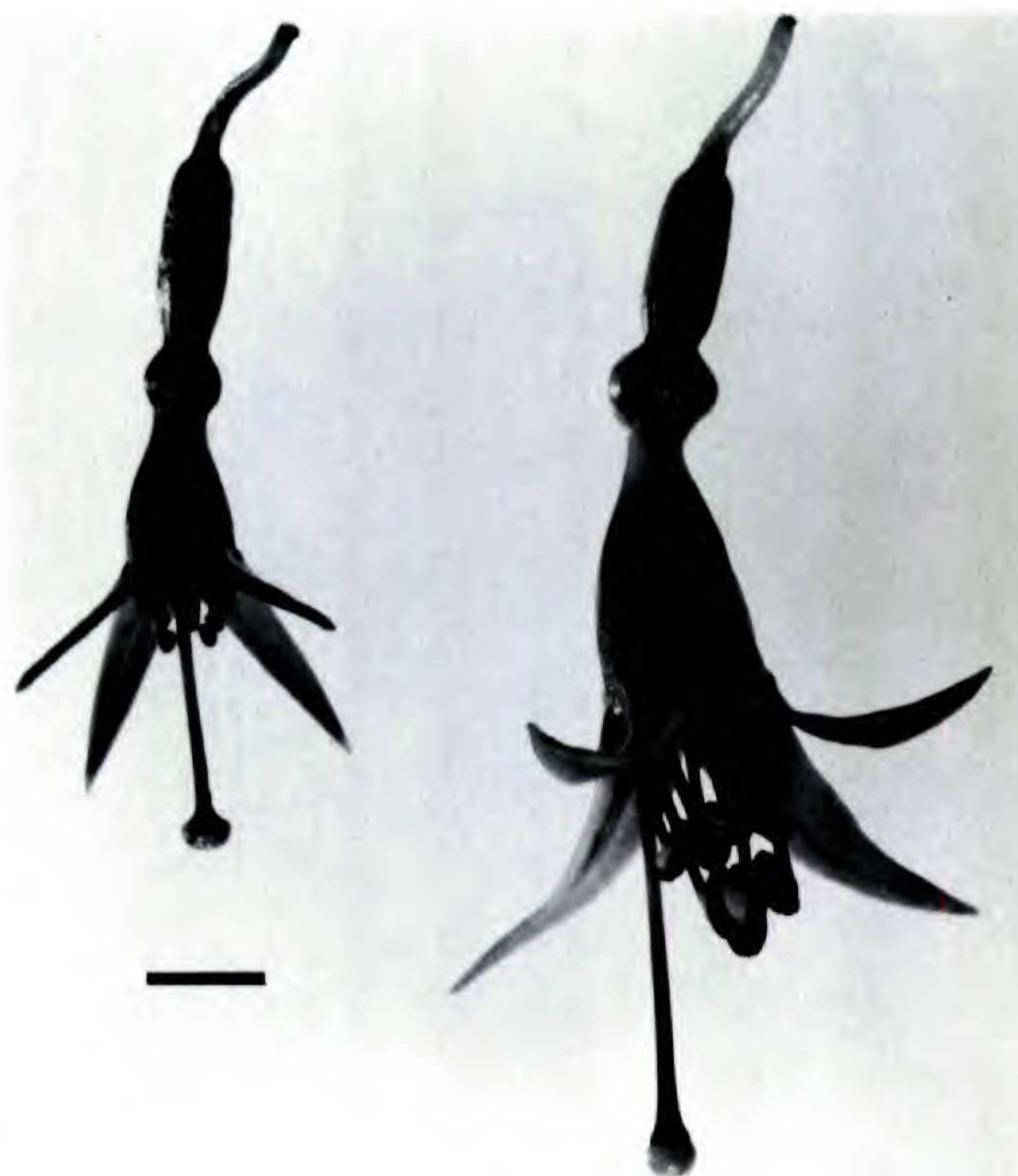
FIGURE 8. Floral morphs of *Fuchsia excorticata*; left, female; right, hermaphrodite. Scale bar = 5 mm. Photograph by R. Lamberts.

(Fig. 9). However, unlike these two species, the floral tube is not dilated at the base.

Fuchsia procumbens. This species stands apart from the other three in that the flowers are erect, yellow-tubed (not dilated at the base), apetalous, with the two whorls of anthers at almost the same level, and with only one-third to one-tenth the number of ovules. Plants are either female, hermaphrodite-male, or male, a situation that was described by Godley (1955) as trioecious. However, Godley (1979) later suggested that a better classification would be into females, males, and inconstant males, with the species then being subdioecious.

Female plants of *Fuchsia procumbens* are constant in their sex expression, with the female flowers approximately two-thirds the size of hermaphroditic and male flowers. Due to the tiny staminodes, the style is exserted with its large, globose stigma (Fig. 10); this led Kirk to classify the flower as "long-styled" (Kirk, 1893).

Plants of *Fuchsia procumbens* with only hermaphrodite flowers have never been found. When hermaphroditic flowers do occur, they are mixed with male flowers on hermaphrodite-male plants, but such plants are uncommon in nature. Hermaphroditic flowers are self-fertile, with the large, globose stigma situated at the same level as the anthers. They are also much less common than male flowers on the same plant. In the latter half
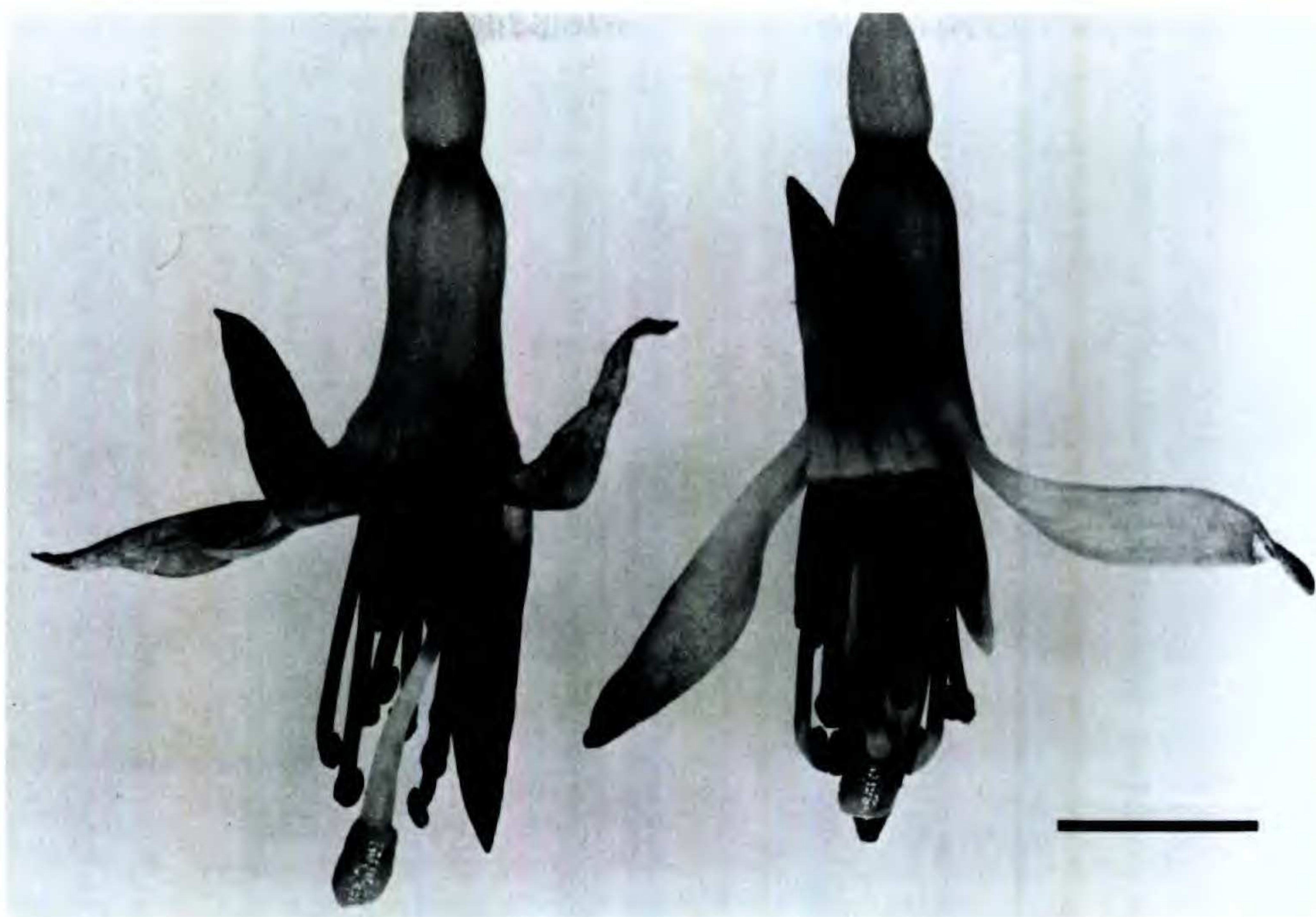
FIGURE 9.   Flowers of *Fuchsia cyrtandroides*. Scale bar = 10 mm. Photograph by R. Lamberts.

of the 1950 to 1951 flowering season, from 5 December to 13 February, a single plant of *F. procumbens* produced 16 hermaphrodite flowers to 152 male flowers (data courtesy of S. D. Baker on a plant cultivated by J. M. Dingley in Auckland). Holdsworth (1959) showed that over a flowering season there is no recognizable trend in the proportion of the hermaphrodite and male flowers.

Maleness in *F. procumbens* is simply due to the lack of a stigma, and male flowers have ovules that are similar in size and number to those of females and hermaphrodites (Table 1). The style length var-
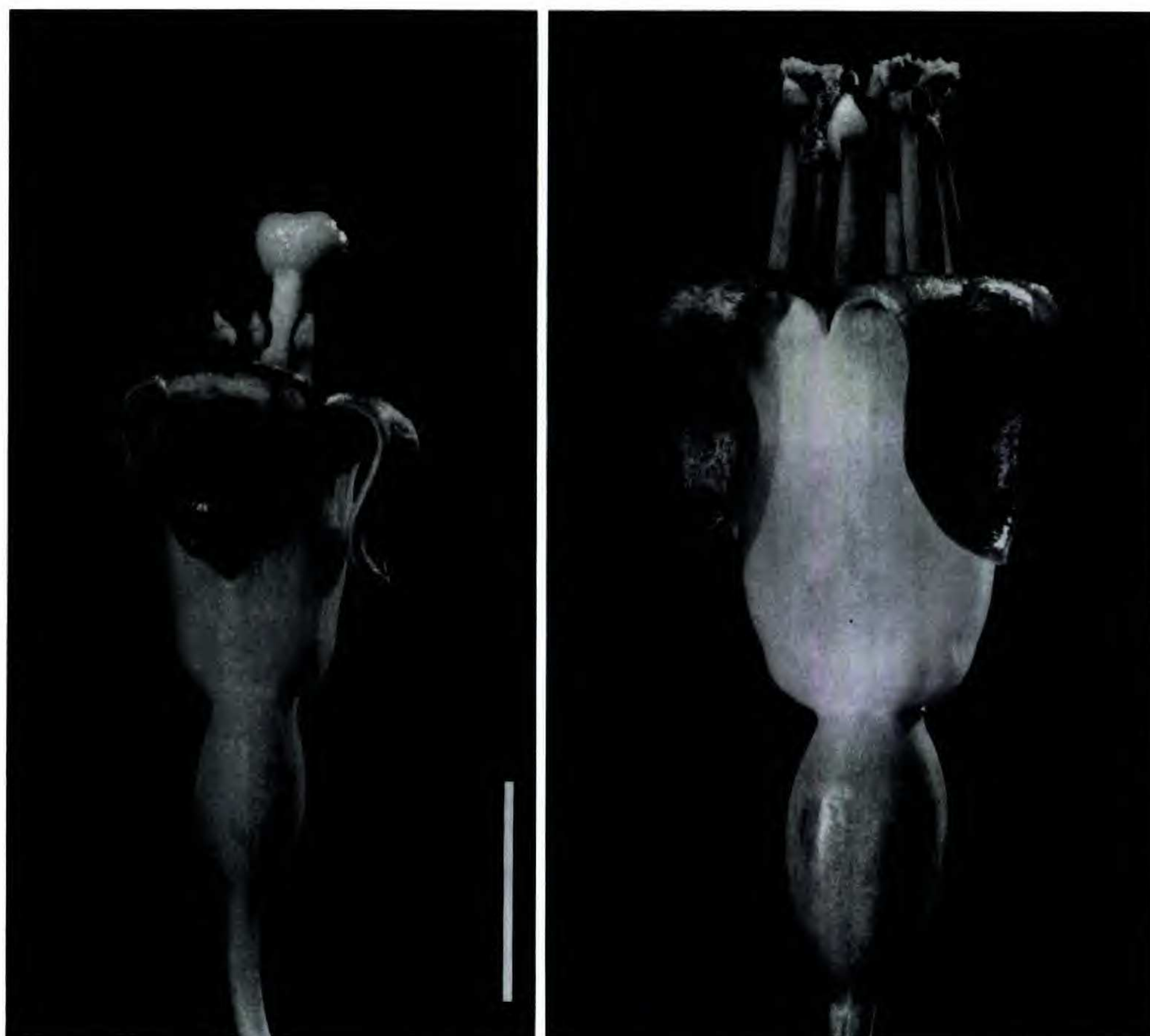
FIGURES 10, 11.—10 (left). Female flower of *Fuchsia procumbens*. Scale bar = 5 mm.—11 (right). Male flower of *Fuchsia procumbens*. Scale is the same as for Figure 10. The hermaphrodite flower differs only in having a well-developed stigma within the ring of anthers. Photographed by C. J. Miles.

Table 1. Ovule numbers in different sexual morphs of *Fuchsia procumbens* (5 flowers per plant).

Sex						Average	Voucher, source locality
Male	127	145	162	207[a]	230[a]	174.2	G2209, Matapouri
Male	90	102	109	131	188	124.0	G2208, Matapouri
Male	92[b]	125	133	141	155	129.2	G2207, Houhora
Male	76	99	121	125	128	109.8	G2201, Houhora
Male	75	81	90	138	140	104.8	G2204, Ngahau
Male	100	106	121	130	131	117.6	G1785, Whangaruru
Male	102	104	107	107	114	106.8	G1786, Whangaruru
Male	51[b]	65	80	82	105	76.6	G2202, Whangarei Heads
Female	80	88	96	97	109	94.0	G2211, Ngawae
Female	117	118	120	124	137	123.2	G1787, Whangaruru
Female	88	98	101	104	116	101.4	G2210, Coromandel
Hermaphrodite-male	76	99	121	125	128	109.8	G2205, Dingley (cultivated)

[a] Fruit with six locules.
[b] Fruit with three locules.

ies from the level of the anthers, as in hermaphroditic flowers, down to the length of the tube. Thus the "mid-" and "short-styled" flowers of Kirk (1893) can occur on the same plant. Male plants are the most common of the three kinds in the wild, with the style usually reaching no further than the mouth of the tube (Fig. 11; such plants were originally called *Fuchsia kirkii*). When Beuzenberg (1966) treated a constant male with gibberellic acid, a normal stigma developed, and a selfed progeny was obtained. In male flowers, the four bundles in the style remain unlignified, and this could be the cause or the result of the acephalic style.

Inheritance of male sterility. In the subdioecious *F. procumbens*, the female is heterogametic with male sterility controlled by a single dominant gene (Godley, 1963). That the same situation occurs in *F. excorticata* was shown by hand pollination of three trees growing in the Kaituna Valley, Banks Peninsula. When selfed, trees 1 and 2 (both hermaphrodites), produced 11 and 30 hermaphrodites, respectively, with no females. Crosses between tree 3 (female) and tree 1 produced 9 hermaphrodites and 12 females; tree 3 × tree 2 gave 60 hermaphrodites and 65 females. Progenies resulting from open pollination were also reared from each tree, with tree 1 producing 21 hermaphrodites, tree 2 giving 42 hermaphrodites, and tree 3 producing 23 hermaphrodites and 23 females.

A different genetic control of male sterility occurs in section *Encliandra* of Mexico and Central America. A statement by Breedlove (1969) shows that in *F. microphylla* HBK and *F. thymifolia* HBK it is the hermaphrodite that is the heterogametic sex, and also that the genetic basis of male sterility is not as simple as in the South Pacific fuchsias.

Breedlove reported that selfed hermaphrodite plants gave progeny with "approximately 50%" of females. Even though lower proportions of females were obtained by Arroyo & Raven (1975) in *F. thymifolia* (42.9%) and *F. microphylla* (34.6%), when hermaphrodite plants were self-fertilized, these proportions are still much higher than the 25% expected if male sterility were controlled by a single recessive gene.

Floral pigments. In an extensive study of flower color pigments in *Fuchsia*, Crowden et al. (1977) found the 3-glucosides and 3,5-diglucosides of the six common anthocyanins to account for nearly all flower color in the genus. However, no detectable levels of the orange-producing pigment pelargonidin were found in flowers of *F. excorticata* and *F. procumbens*, which were characterized mainly by a combination of malvidin, peonidin, and petunidin. The characteristic purple anthers of *F. excorticata* were rich in petudinin, malvidin, and cyanidin. Preliminary analysis of the blue pollen of *F. excorticata* shows it to be a bound anthocyanin, probably forming a blue metallo-flavone-anthocyanin complex in living flowers (N. H. Fischer, pers. comm. to P. Raven in September 1988).

Pollen. *Fuchsia* pollen has been well studied by Nowicke et al. (1984), Praglowski et al. (1983), and Skvarla et al. (1976). The New Zealand species were also treated by Moar (1993). Besides having the unique suite of onagraceous pollen features such as viscin threads, protruding apertures, paracrystalline-spongy ektexine, and solid endexine, *Fuchsia* pollen is distinctive in its predominantly 2-aperturate grains with wide and short colpi or pores. Furthermore, the grains are always shed sin-

gly. Within the genus, the South Pacific fuchsias are generalized in features such as the 2-aperturate grains, segmented-beaded viscin threads, and globular type of ektexine sculpture. While the pollen of the South Pacific species of *Fuchsia* is considerably smaller than the American species (Praglowski et al., 1983), and some of the American species have other distinguishing characters such as smooth viscin threads or 3-aperturate grains, it is not possible to distinguish between any of the South Pacific *Fuchsia* species by pollen alone (Daghlian et al., 1985).

Fossil *Fuchsia* pollen is known from New Zealand from as early as the late Oligocene, around 27 mya (Mildenhall, 1980), and then extends up to the Pliocene and possibly into the Quaternary (Pocknall & Mildenhall, 1984). Although the fossil grains have been assigned to *Diporites aspis* Pocknall & Mildenhall, detailed ultrastructural analysis by Daghlian et al. (1985) has shown that they clearly represent *Fuchsia* pollen. Recently, fossil *Fuchsia* pollen dating back to the early Oligocene (at least 35 mya) has been documented from eastern Australia; these findings represent the oldest fossil records of the genus. The most recent records of fossil pollen in Australia, however, extend only to the middle Miocene, about 15 mya (Berry et al., 1990). Thus, it is likely that *Fuchsia* was once widespread at least in eastern Australia but went extinct there as the continent moved steadily northward and entered into increasingly more arid climatic zones.

POLLINATION

Fuchsia excorticata is well known to be pollinated by honeyeater birds (Meliphagidae) in New Zealand (Potts, 1871; Kirk, 1893; Thomson, 1927; Godley, 1979; Craig et al., 1981; Delph & Lively, 1985). The main visitors are the bellbird (*Anthornis melanura*) and the tui (*Prosthemadera novae-zelandiae*), although the rare stitchbird (*Pogonornis cincta*), which is now confined to Hen, Cuvier, and Little Barrier Islands (Bartle & Sagar, 1987), has been reported to visit *Fuchsia* in the north (Kirk, 1893). During the flowering season, blue *Fuchsia* pollen can conspicuously cover the birds' foreheads, which was first noted by Potts (1871) in bellbirds. Birds such as silvereyes (*Zosterops lateralis*), as well as bumblebees (*Bombus* spp.), also feed off the flowers of *F. excorticata*, but they rob the nectar without much effect upon pollination (Delph & Lively, 1985).

The flowers of *F.* ×*colensoi* and *F. perscandens* are similar to those of *F. excorticata*, but pollinators have not been recorded on them. In the shrub form of *F. perscandens* it would be difficult for birds to reach the flowers, which are usually produced inside the tangle of wiry branches.

On Tahiti no native birds have been observed on the flowers of *F. cyrtandroides*. However, silvereyes (*Zosterops lateralis*), which were first observed on the island (self-introduced?) in 1939 (Holyoak, 1974), were observed on *F. cyrtandroides* "flying from flower to flower, probably searching for nectar" in September 1971 (M. van Balgooy, pers. comm. to P. Raven). Since *F. cyrtandroides* is hermaphroditic, it is probably able to produce selfed seed as well. Meliphagid birds are not represented on the list of known extinct Tahitian birds by Holyoak (1974).

Despite close observation of native populations of *F. procumbens* by K. Reynolds, E. Godley, and T. Raven, no pollinator activity has been seen. None of the bird pollinators of *F. excorticata* has been seen visiting the flowers of *F. procumbens*, nor have any other birds. We should note, however, that the bellbird is extremely rare in the North Auckland sector where *F. procumbens* occurs. Thus Buller (1878) received first-hand reports from Whangarei that, "In 1859 this bird was very abundant, in 1860 it was less numerous, in 1862 it was extremely rare, and from 1863 to 1866 I never saw but one individual. It now seems to be entirely extinct in the district." With regard to the possibility that earlier bird pollinators of *F. procumbens* are now extinct, with the exception of subfossil remains of tui, bellbird, and stitchbird, there are no records of fossil Meliphagidae in New Zealand. Among other extinct birds, there are likewise none which could reasonably be suggested as possible pollinators (P. R. Millener, pers. comm.).

On the Poor Knights islands off the North Auckland coast, where bellbirds occur (Bartle & Sagar, 1987) but *Fuchsia procumbens* does not, geckoes in the genus *Hoplodactylus* regularly take nectar from three coastal plant species and are dusted with pollen (Whitaker, 1968, 1987). It has been suggested that lizards could pollinate *F. procumbens* on the mainland (E. K. Reynolds, pers. comm. to E. Godley, Dec. 1979 and to P. Raven, Oct. 1980; Whitaker, 1987). However, at Deep Water Cove, Cape Brett Peninsula, where skinks are plentiful (e.g., Lizard Bay), no pollinator activity on *F. procumbens* was observed by Mrs. Reynolds and F. J. Newhook, either during the day or throughout one night's observations. At Deep Water Cove, there was a large colony of small native bees near a population of *F. procumbens* (both male and female plants), but no floral visits were made, despite close observation by E. K. Reynolds, F. J. Newhook, and T. Raven.

Mrs. Reynolds has since caught a native bee with blue pollen on it, on a male plant of *F. procumbens* in her garden at Whangarei.

The flowers of all South Pacific species of *Fuchsia* are scentless and produce copious nectar at the base of the floral tubes. The nectar is high in hexoses and low in sucrose, which is consistent with other species pollinated by passerine (perching) birds in both the Old and New Worlds (Baker & Baker, 1979). The following ratios of sucrose to hexoses (combined glucose and fructose) in New Zealand fuchsias were obtained by Herbert and Irene Baker (unpublished data): 0.098 in *F. procumbens*, 0.059 in *F. excorticata*, and 0.033 in *F. ×colensoi*. The predominantly hummingbird-pollinated American species of *Fuchsia*, on the other hand, have sucrose-rich nectars with ratios ranging from 0.571 to 5.253.

Flower color. The flower color of *F. excorticata* was described by Kirk (1889) as "at first greenish, streaked or blotched with a dull deep purple, passing at length into a dull red." Delph & Lively (1985, 1989), who called the first phase green, were the first to study the development and significance of these changes. They found that open flowers of both sexes last an average of 11 days. About halfway through this period, they pass from green-purple to bright red over a transition period of 1 to 2 days. The change is age-dependent and not pollination-induced. Nectar is produced only during the initial green-purple phase, when pollination occurs. Delph & Lively (1989) suggested that red flowers, which are post-reproductive, act as a cue to direct pollinators away to the potentially reproductive green-purple flowers.

Flowers of both *Fuchsia perscandens* and *F. ×colensoi* exhibit the same color change pattern as *F. excorticata*. In 1988, P. Berry was able to confirm in Tahiti that native-growing plants of *Fuchsia cyrtandroides* also exhibit two different color phases; its flowers change during anthesis from a dull green with purple streaks to a uniform deep purple. Only *F. procumbens* differs fundamentally from the other South Pacific species. It passes gradually from a uniform green in bud to a yellowish floral tube during anthesis; the sepal lobes reflex back completely against the tube and turn a contrasting dull purple. Thus, there appears to be no clear separation in this species between the reproductive and post-reproductive phases of the flower. This may be due to a longer period of anthesis in *F. procumbens* than in the other species in the section, and detailed observations would be welcome on the length of
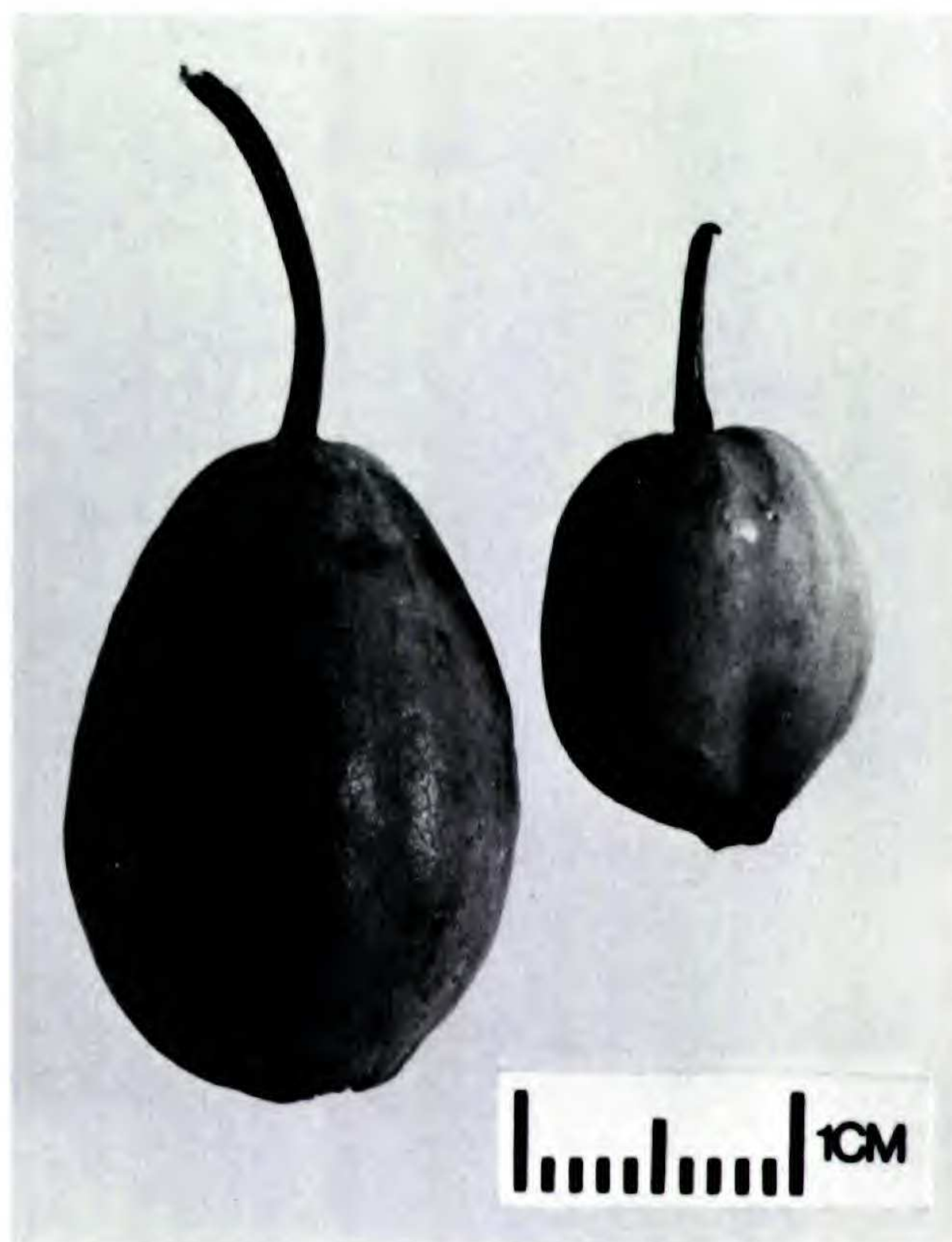
FIGURE 12. Berry of *Fuchsia procumbens*. Photograph by R. Lamberts.

anthesis and progression of color change in this species.

FRUITS AND DISPERSAL

As with the flowers, the fruit of *Fuchsia procumbens* is distinct from that of the other three South Pacific species. This species produces a hollow, red, elliptic berry, up to 2.5 × 1.6 cm, with a fleshy pericarp 2–3 mm thick and thinner septa (Figs. 12, 13). At the inner angle of each of the four hollow locules there are two rows of seeds attached to the central fleshy axis, which is ca. 1 mm in diameter. Seed numbers in nine fruits resulting from natural self-pollination of an hermaphrodite-male plant with ovule numbers from 76 to 128 (see Table 1) were: 17, 29, 32, 42, 44, 44, 59, and 73. In a later year six fruits gave 28, 40, 59, 60, 66, and 69 seeds. Parthenocarpic fruits, smaller than normal, are produced when pollen is applied to the acephalic style of the male plant (Godley, 1955, 1979) or in isolated female populations (Godley and Reynolds, unpublished manuscript).

The fruits of the other South Pacific species are smaller, more fleshy, more uniformly globoid or oblong, purple when ripe instead of red, and with multiseriate ovules embedded in pulp in each locule. They have about 10 to 20 times the number of seeds as *F. procumbens*, and the seeds are much smaller. Parthenocarpy has not been observed in
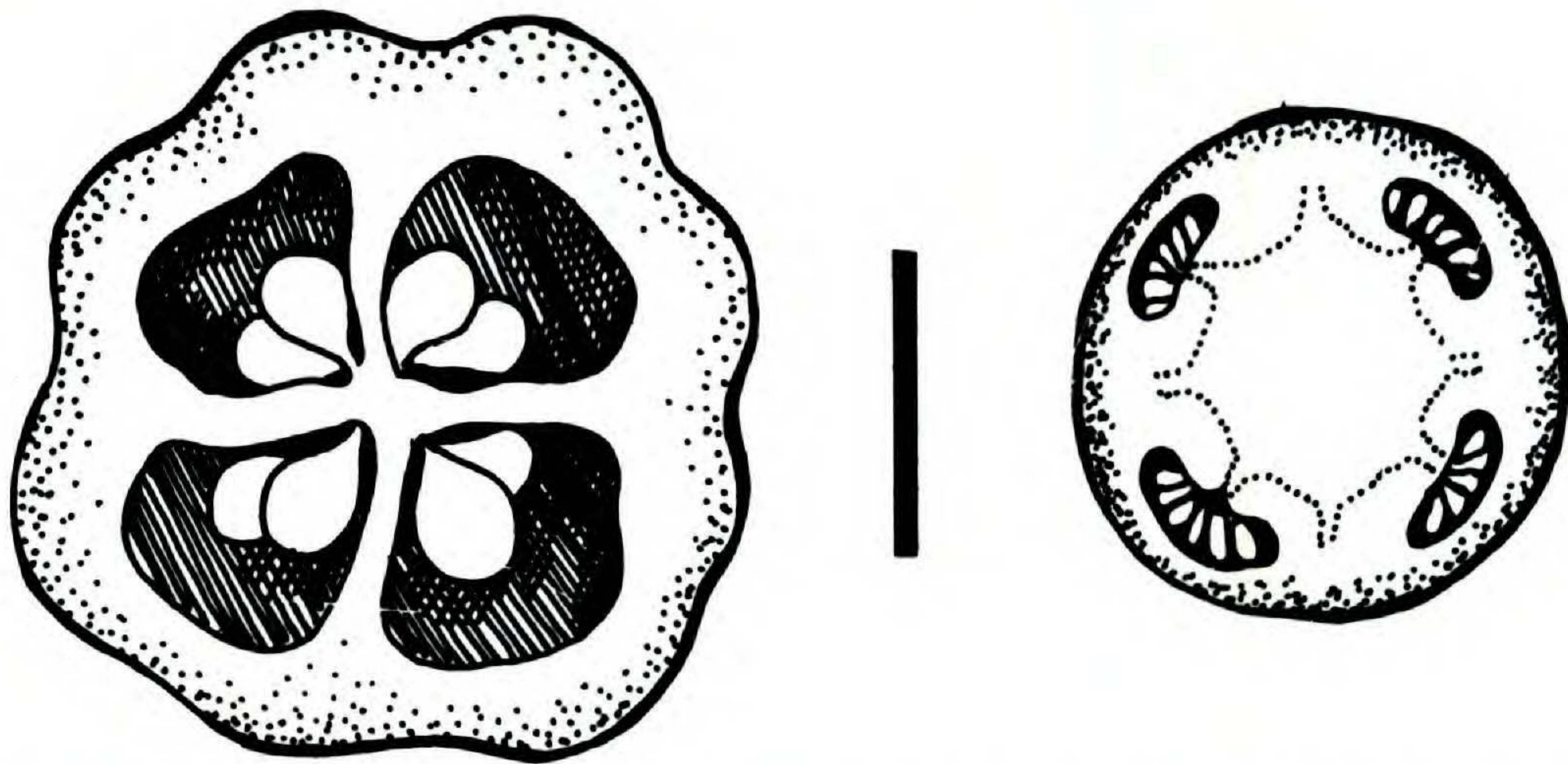
FIGURE 13. Cross sections of fruits of *Fuchsia procumbens* (left) and *F. excorticata* (right). Scale bar = 5 mm. Drawing by P. A. Brooke.

any of the other South Pacific species. The berry of *F. excorticata* is oblong, purplish black, and up to 1.5 × 0.7 cm. It is fully fleshy, with the pericarp, septa, and placentae filling the fruit, except for the four peripheral groups of very small imbedded seeds (Figs. 13, 14). Seed numbers and germination rates six weeks after sowing are given in Table 2. The overall germination after six weeks was 62.2%. The berry of *F. perscandens* is a smaller version of *F. excorticata*, while *F. cyrtandroides* can be distinguished by the shape of the apex and the tapering base (Fig. 15). Two fruits of the latter derived from hand-pollinations measured 1.5 × 1.0 cm with 568 seeds (from selfing) and 1.0 × 0.7 cm with 576 seeds (from crossing).

Dispersal. Berries of *Fuchsia excorticata* (konini,

in Maori) are eaten freely and dispersed by the native New Zealand pigeon (*Hemiphaga novae-zelandiae*; Cockayne, 1928; McEwan, 1978) and other birds. On Kapiti Island tuis eat the konini, while bellbirds do not even wait until the berries are ripe, but eat them as soon as they show color (Wilkinson, 1952). In Dunedin, Thomson (1901) noted that *F. excorticata* became more abundant in the Town Belt with the increase of introduced blackbirds (*Turdus merula*) and thrushes (*Turdus philomelos*). These same birds are likely to eat and disperse the very similar berries of *F. perscandens* and *F. ×colensoi. Fuchsia cyrtandroides* also has juicy, many-seeded berries, but their possible dispersal agents in Tahiti are unknown and may have included birds that were driven extinct after human colonization. Dur-

FIGURES 14, 15. Berries of *Fuchsia excorticata* (left two, Fig. 14) and *Fuchsia cyrtandroides* (right two, Fig. 15). Scale bar is divided in 1 mm units. Photographs by R. Lamberts.

Table 2. Seed numbers and germination rates in fruits of *Fuchsia excorticata*.

	Average seed number per fruit	Range	Average germination percentage	Number of fruits
Plant 1 (hermaphrodite) selfed	475	324–552	67.5	9
Plant 2 (hermaphrodite) selfed	662		47.3	1
Plant 2 × plant 1	602	563–641	65.2	5
Plant 3 (female) × plant 1	489	398–550	67.0	5
Plant 3 × plant 2	539	395–614	56.0	10

ing a visit by P. Berry to native populations of *F. cyrtandroides* in February 1988, a number of trees with mature fruits were seen, but there were no signs of fruit removal by birds or other animals. Some berries were found still attached to the branches, but they were completely dried out and split open to expose the tiny seeds. *Fuchsia procumbens* is unusual in its larger, more leathery, fewer-seeded, and longer-lasting fruits, but nothing is known about its dispersal mechanism.

SEED MORPHOLOGY AND ANATOMY[4]

To assess differences in seed morphology and anatomy in the South Pacific species of *Fuchsia*, the following specimens were examined: *Fuchsia cyrtandroides* (*Fosberg 61078*, US), *F. excorticata* (*Walker 4317*, MO), *F. perscandens* (*Raven & Simpson 25567*, MO), and *F. procumbens* (*Engelhorn 25719*, MO). Overall seed shape and seed surface morphology were observed using a Hitachi S2050 scanning electron microscope at 10 and 15kV. Dry seeds were soaked once in water and dehydrated through an ethanol series, critical-point dried in CO_2, and coated with platinum. For anatomical study, dry seeds were soaked once in FAA (5:5:90, using 50% ethanol), dehydrated through a t-butyl alcohol series, and embedded in Paraplast with a melting point of 56–58°C. The seeds were sectioned with a rotary microtome following standard paraffin methods. Sections cut at 8–10μ thickness were stained with Heidenhain's hematoxylin, safranin, and fastgreen FCF, and mounted with Entellan.

In all four species studied, mature seeds are slightly curved and ellipsoid or broadly ovoid with a small raphe. Seed sizes, based on measurements of five seeds in each species, are as follows: 1.10–1.14 mm long and 0.52–0.64 mm wide (between raphe and antiraphe) in *Fuchsia cyrtandroides*, 0.77–0.88 mm long and 0.39–0.46 mm wide in *F. excorticata*, 0.83–0.96 mm long and 0.52–0.63 mm

wide in *F. perscandens*, and 2.39–2.43 mm long and 1.26–1.43 mm wide in *F. procumbens* (Figs. 16, 19, 22, and 25). Seed surface is scalariform in *Fuchsia cyrtandroides*, *F. excorticata*, and *F. perscandens*, but reticulate-foveate in *F. procumbens*.

The mature seeds of all four species are exalbuminous, as are all other species of *Fuchsia* and Onagraceae in general. The seed coat is typical of other members of the genus, composed of an exotesta, a multi-cell-layered mesotesta, and endotesta, a fibrous exotegmen, and an endotegmen (Figs. 17, 18, 20, 21, 23, 24, 26, 27, and 28). In all four species the cells of the exotesta are characteristically enlarged, while cells of the meso- and the endotesta are much smaller. The mesotesta is three- to five-cell-layered except in *Fuchsia excorticata*, where it is two- to three-cell-layered. The cells of the mesotesta are densely tanniferous except in *Fuchsia procumbens*. The cells of the endotesta are relatively clearly distinguished from the mesotestal cells in *Fuchsia cyrtandroides*, *F. excorticata*, and *F. perscandens* because they are thick-walled and contain crystals, but they are hardly distinguished from the mesotestal cells in *F. procumbens* because of the lack of such features.

Cells of the fibrous exotegmen are longitudinally elongate. They are narrow and about 2–5μ thick in *Fuchsia cyrtandroides*, *F. excorticata*, and *F. perscandens* (Figs. 18, 21, 24), but are extremely wide and about 30–40μ thick in *F. procumbens* (Figs. 27, 28). Cells of the endotegmen appear circumferentially elongate and thus criss-cross with longitudinally elongate exotegmic cells, and they are always tanniferous.

On the basis of seed morphology and anatomy, the four South Pacific species of *Fuchsia* are characterized by their enlarged exotestal cells, which is an apomorphic character not found anywhere else in the genus. Within this group, *Fuchsia procumbens* is clearly distinct from the others in seed size and seed surface sculpturing, as well as in the thickness of the fibrous exotegmen. *Fuchsia cyrtandroides*, *F. excorticata*, and *F. perscandens* can be

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[4] Hiroshi Tobe, Kyoto University, Kyoto 606-01, Japan.

distinguished from each other by seed size and thickness of the mesotesta, but they closely resemble each other in sharing small seeds with a tanniferous mesotesta.

SEEDLINGS

In *Fuchsia excorticata*, the cotyledons are epigeal with a hypocotyl 5–7 mm long. They are glabrous, entire, without obvious veins, green on both surfaces, and reach a length of 3 mm. Their shape is roughly deltoid with a slight shoulder on the upper half of each lateral margin. Observations on 5 seedlings showed that pairs of opposite and decussate leaves are produced at the first few nodes, followed by subopposite pairs in which the leaves are offset vertically from 2 to 8 mm. The sequence of opposite and subopposite nodes was as follows: 2+5, 3+5, 4+4, 5+4. In the fifth seedling, however, the leaves were opposite at nodes 1–3 and 5–6, but subopposite at 4 and 7. From then on, the leaves are produced singly at each node and are evenly spaced with a phyllotaxis of approximately ⅖. The margins of the first leaves show small, spaced teeth not seen in the later leaves, while the undersurface of the first pair of leaves resembles that of the adult leaf in being silver-white tinged with pink. Tiny leaves begin to appear on very short shoots in the axils of the cotyledons after the first three pairs of leaves have been produced (about 50 days after germination), followed consecutively by buds in the axils of the upper leaves. Cotyledons of *F. perscandens* seen at Macdonald Downs, North Canterbury, in March 1988, were similar to *F. excorticata*.

In *Fuchsia cyrtandroides*, the cotyledons are similar in size and shape to those of *F. excorticata* but bear scattered hairs. In contrast to *F. excorticata*, the seedling leaves have shorter petioles, are more elliptic, and are always opposite and decussate.

Despite its small adult size, *Fuchsia procumbens* has the largest seeds and cotyledons of the native South Pacific fuchsias. Its cotyledons differ from *F. excorticata* in having a more flattened stalk, reaching 5 mm long, and a blade that is 5 mm long and 5 mm at the widest point. On a 2-month-old seedling, the main stem was 25 mm long, the hypocotyl 10 mm long and almost 1 mm thick, and the main root 45 mm long with abundant development of secondary roots, giving a root system 9 cm long when extended. The pair of cotyledons and the pairs of leaves at the four subsequent nodes were opposite and decussate; lateral shoots had developed in the axils of the cotyledons and the first two pairs of leaves. These lateral shoots bore opposite pairs of

leaves for at least the first two nodes. The main changes in a 3-month-old seedling were: (a) the main stem began to bend over, and the new leaves produced beyond the third or fourth node were subopposite and later alternate, with the same change in lateral shoots, and (b) secondary lateral shoots appeared at the cotyledon nodes and the first two leaf nodes. These grew out horizontally between the primary lateral shoot above and the cotyledon or leaf below, and further emphasized the procumbent growth form which had begun to develop.

The main conclusion from these observations is that seedlings of the South Pacific fuchsias begin with opposite and decussate leaves, but only in *Fuchsia cyrtandroides* is this leaf arrangement found in the adult. If opposite leaves are considered primitive in the Onagraceae (fide Raven in Cronquist, 1981), then *F. cyrtandroides* may be plesiomorphic in this respect. Second, the presence of secondary shoots in the axils of *F. procumbens* seedlings is an example of the basis for Willis's (1925) statement that many fuchsias "show two buds in each axil, one above the other."

LEAF ANATOMY AND FOLIAR FLAVONOIDS

The leaf anatomy of *F. excorticata* (Table 3) shows no xerophytic features. A cuticle is either absent or poorly developed, and the stomata are not sunken or otherwise protected. The outstanding feature is the absence of chlorophyll in the spongy parenchyma, which makes up the lower ⅔ of the leaf, leading to the silvery color of the lower leaf surface (Suckling, 1914).

In *Fuchsia perscandens*, the main differences in leaf anatomy from *F. excorticata* are that the palisade tissue is only 1-layered in the much smaller and thinner leaf and that chlorophyll is present in the spongy parenchyma (Table 3).

Foliar flavonoids have been well characterized for all sections and most species of *Fuchsia*, as a result of the broad surveys by Averett & Raven (1984) and Averett et al. (1986). Williams et al. (1983) also analyzed a set of six *Fuchsia* cultivars, and Williams & Garnock-Jones (1986) examined the different members of section *Skinnera*. These results show that all species of *Fuchsia* contain flavonol-3-O-glucosides based on quercetin and kaempferol. Flavone glycosides occur in only nine species belonging to five sections, but all four South Pacific species of *Fuchsia* are characterized by the presence of flavones. Furthermore, flavone sulphates, which are found nowhere else in the genus, are known from all South Pacific species of *Fuchsia* except *F. cyrtandroides*.
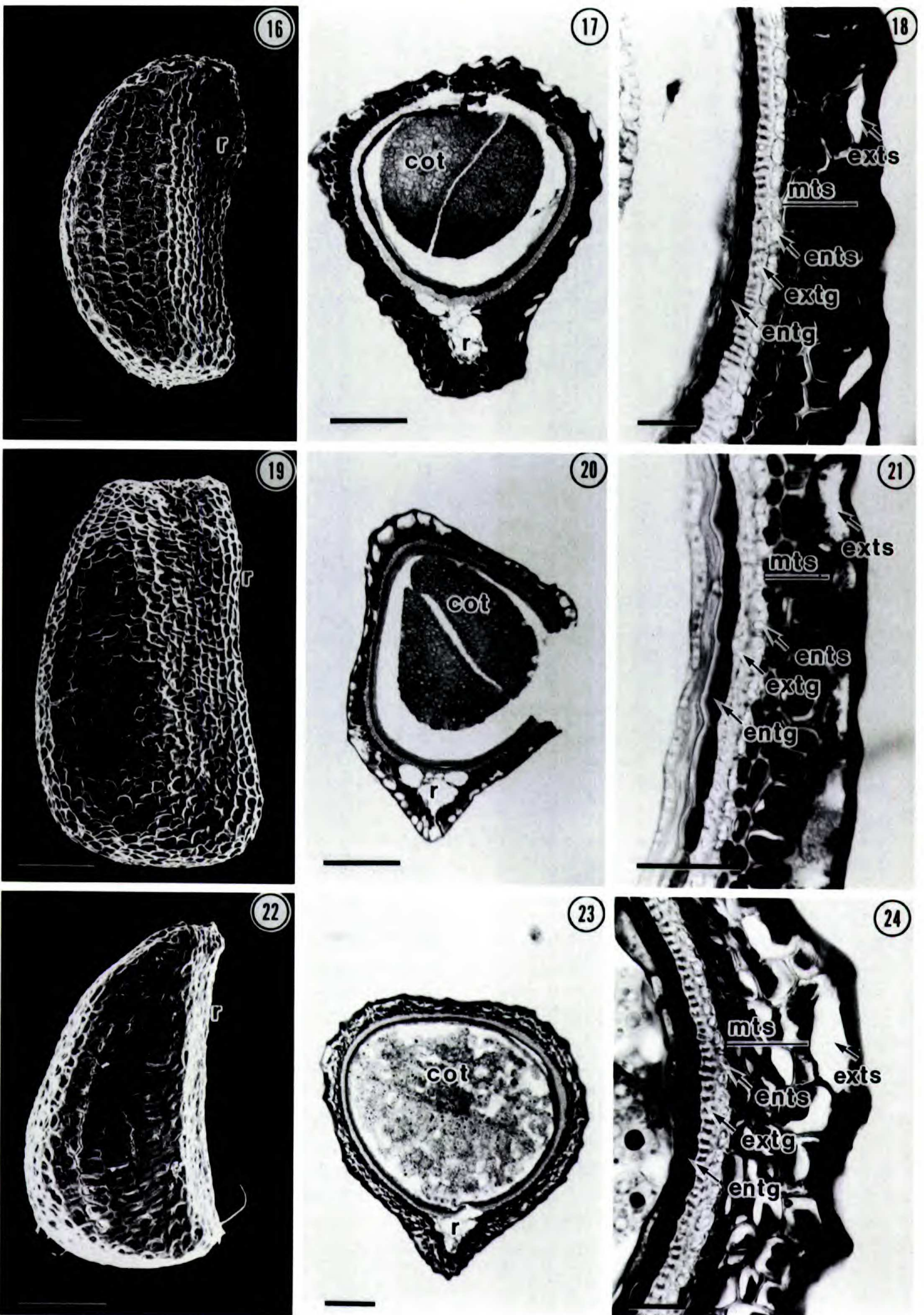
FIGURES 16–24.   Morphology and anatomy of mature seeds of the *Fuchsia* sect. *Skinnera.*—16, 19, 22. Scanning electron micrographs of entire seeds (scale = 200μ).—17, 20, 23. Transverse sections of entire seeds (scale = 100μ).— 18, 21, 24. Transverse sections of seed coat (scale = 20μ). 16–18. *F. cyrtandroides.* 19–21. *F. excorticata.* 22–24. *F.*

CYTOLOGY

Chromosome counts have been made for all South Pacific taxa of *Fuchsia* (Table 4; Figs. 29–32), showing them to be uniform in chromosome number, with $n = 11$. This is the basic chromosome number for both the genus (Berry, 1982) and the family (Raven, 1979a). Meiosis was also analyzed in several artificial hybrids involving *F. procumbens* and the other two New Zealand species (Table 4; Figs. 30–32). Pairing was normal except in one individual of *F. procumbens* × *F. excorticata*, in which there were two univalents.

ARTIFICIAL CROSSES

A series of artificial crosses was made in Lincoln, outside Christchurch, New Zealand, with results presented in Table 5. The crosses in 1951–1952 and 1990–1991 were done by E. Godley, and those in 1969–1973 were done by his assistant, Diane H. Smith.

Fuchsia procumbens × *F. excorticata* (Table 5). In four separate crosses, 29 flowers gave 18 fruits and yielded 783 seeds. Cross 1969/1 differed from the others in that the pollen (collected on 14 October) was used over five days on three occasions. Pollen used on 15 October to pollinate eight flowers produced two fruits; when used on 16 October, one fruit resulted from three flowers pollinated; and on 20 October, all four flowers pollinated produced fruit, which may indicate a higher viability for the older pollen. The cross with *F. excorticata* as the female parent (cross 1952/1) gave a much greater number of seeds per fruit than when *F. procumbens* was the female, presumably because of the much greater number of ovules in *F. excorticata*. Likewise, fruit size in crosses where *F. procumbens* was the female parent was much greater than when *F. excorticata* was the pollen recipient, reflecting the much larger size of *procumbens* fruits. When female plants of *F. procumbens* were used as pollen recipients, seed germination was much higher than when hermaphroditic flowers were used from hermaphrodite-male plants.
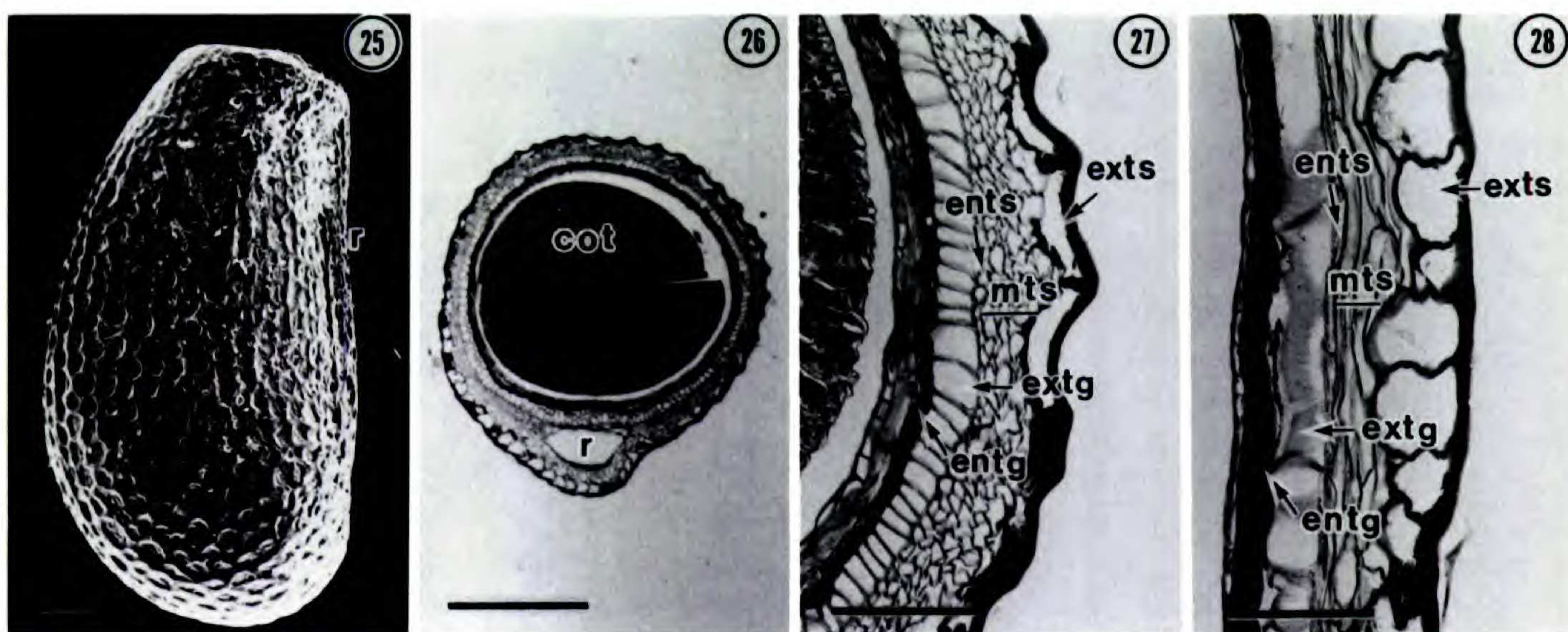
Seedlings from cross 1951/6 (*procumbens* × *excorticata*) were given to H. H. Allan in Wellington, who wrote, "In their second year the plants are erect shrubs with spreading branches" (Allan, 1961). The leaves of an eight-year-old plant grown at Lincoln were intermediate in size and shape between the parents. The flowers showed a slight swelling at the base of the floral tube, derived from *F. excorticata*, and the calyx lobes were reflexed as in *F. procumbens*. As females of *F. procumbens* are heterozygous for the dominant gene for male sterility, and hermaphrodites of *F. excorticata* are homozygous recessive, these crosses gave plants with either female or hermaphrodite flowers. In both types, the style protruded for varying lengths beyond the staminodes or stamens. N. T. Moar reported in October 1958 that the total pollen grains on each of two slides from a hermaphrodite were 63 and 121, with viable grains at 16% and 17%, respectively. A sample from *F. procumbens* (Ngawae) gave 66% viable pollen.

When plants of cross 1969/1 were four years old, leaf blade dimensions ranged from 3.0 × 1.5 cm to 4.7 × 3.0 cm (a leaf from each individual was pressed and mounted as CHR 194409 A–H). The first flowers were observed on 18 January 1974, and during the first flowering season, there were 20 female and 8 hermaphrodite plants. The number of petals on these plants varied from zero to four. An hermaphroditic plant showed either perfect pairing at meiosis or else ten bivalents and two univalents (Figs. 31, 32; Table 4).

Fuchsia procumbens × *F. perscandens* (Table 5). In cross 1969/2, pollination was spread over eight days, but fresh pollen from a nearby source was used for each batch. Approximately 41% of the seed from the 15 fruits that were produced were separated as "bad," and these 207 seeds when sown separately gave only 12 seedlings. The remaining 294 seeds gave 71.7% germination. In four-month-old plants the main central stem had turned over and was prostrate, at least near the tip. As with *F. procumbens*, the secondary branches (up to 5–7) became prostrate and much longer (up to 60 cm long). In a few five-month-old plants, the secondary prostrate branches were only about 30 cm long, and there were several secondary shoots up to 8 cm high on the crown of the plant. The first hybrid to flower was observed almost precisely one year after seeds were sown, and the second plant flowered one month later. Both plants bore female flowers, similar to *F. procumbens* × *F. excorticata*. Meiosis in a later-flowering hermaphroditic individual showed 11 bivalents (Fig. 30; Table 4).

←

perscandens. Abbreviations: cot, cotyledons; entg, endotegmen; ents, endotesta; extg, exotegmen; exts, exotesta; mts, mesotesta; r, raphe. Microphotographs by H. Tobe.

FIGURES 25–28. Morphology and anatomy of mature seeds of *Fuchsia procumbens*.—25. Scanning electron micrograph of entire seed (scale = 200μ).—26. Transverse section of entire seed (scale = 500μ).—27. Transverse section of seed coat (scale = 100μ).—28. Longitudinal section of seed coat (scale = 100μ). Abbreviations same as in Figures 16–24. Microphotographs by H. Tobe.

Fuchsia excorticata × *F. perscandens* (Table 5). In cross 1969/3, although 16 flowers were pollinated with fresh pollen in three batches, only one fruit was collected, and it was suspected that birds had eaten any others. Of the 76 seeds sown on 26 February 1970, 42 had germinated by 15 March. However, most young seedlings died by 1 April, and the only survivors were three seedlings which came from seeds germinated after this time. These plants reached heights of 50, 42, and 27 cm by September 1970.

In cross 1990/1, the contents of a whole fruit were sown, but only two seeds germinated, and these were left growing at Lincoln (accession #G283/91); leaves of the hybrid and parents are shown in Figure 33. Cross 1991/1 was the most successful of this series, with 350 seeds obtained from five of the ten fruits, and 21 plants of the numerous progeny left growing at Lincoln (accession #G54/92).

Fuchsia cyrtandroides × *F. procumbens* and *F.* *perscandens*. Although very few flowers of *F. cyrtandroides* were available to pollinate, crosses with both *F. procumbens* and *F. perscandens* did produce numerous seeds, and in both cases the large ovule numbers of the female parent are reflected in large seed numbers. Robust hybrid plants were obtained from the cross of *F. perscandens* × *F. cyrtandoides*, and these later flowered.

NATURAL HYBRIDS

Fuchsia excorticata and *F. perscandens* have the same geographical range except that *F. perscandens* is not found in the far north nor on Chatham, Stewart, or Auckland Islands. Throughout the range of *F. perscandens*, the two species overlap ecologically so that natural hybridization is possible, and plants intermediate between the two species are regularly collected. R. L. Bieleski reported his impression of the situation of these two species and numerous intermediates after a trek along the Heaphy Track, between Karamea and Bainham on the South Is-

Table 3. Features of the leaf anatomy in South Pacific species of *Fuchsia*.

	Upper epidermis	Palisade tissue	Spongy tissue	Lower epidermis
F. excorticata	2-layered, stomata absent	2 or 3 layers	Chloroplasts absent	1 layer with stomata
F. cyrtandroides	3- or 4-layered, stomata absent	Up to 4 layers	Chloroplasts absent	1 thin layer with stomata
F. perscandens	1 layer, stomata absent	1 layer	Chloroplasts present	1 thin layer with stomata
F. procumbens	1 large layer, stomata absent	1 layer	Chloroplasts present	1 layer?, stomata undulate

Table 4.   Chromosome numbers in the South Pacific species of *Fuchsia*.

Taxon	Chromosome number	Voucher, source locality
Fuchsia excorticata	n = 11	*CHR 200293* (Botanic Gardens, Christchurch)[1]
Fuchsia perscandens	n = 11	*CHR 200301* (Riccarton Bush, Christchurch)[1]
Fuchsia ×colensoi	n = 11	*CHR 200300* (Riccarton Bush, Christchurch)[1]
Fuchsia cyrtandroides	n = 11 n = 11	*Carlquist 653* at DS (Aorai, Tahiti)[2] *Plant G9804/6*[3]
Fuchsia procumbens	n = 11, 2n = 22	*CHR 200302-3* (Cultivated plants, Auckland)[1]
Fuchsia procumbens × *F. excorticata*	n = 11, n = 10 bivalents and 2 univalents	*Cross 1969/1* from Table 5[3]; *CHR 194409 A–H*
Fuchsia procumbens × *F. perscandens*	n = 11	*Plant G8968* from Cross 1969/2 in Table 5[3]

[1] Report by Beuzenberg & Hair (1959).
[2] Counted by P. H. Raven.
[3] Counted by E. J. Beuzenberg.

land, in February 1972: small-leaved, low scrambling plants of *F. perscandens* were found along the alluvial river flats; large silvery-leaved shrubs of *F. excorticata* occurred close to *F. perscandens* but were more numerous on limestone knobs on higher ground; and a variety of "*colensoi*" plants with intermediate growth forms and leaves occurred in coastal flats and in the coastal hedge facing the sea, becoming more and more *excorticata*-like as the path changed to traverse granite heads and valleys
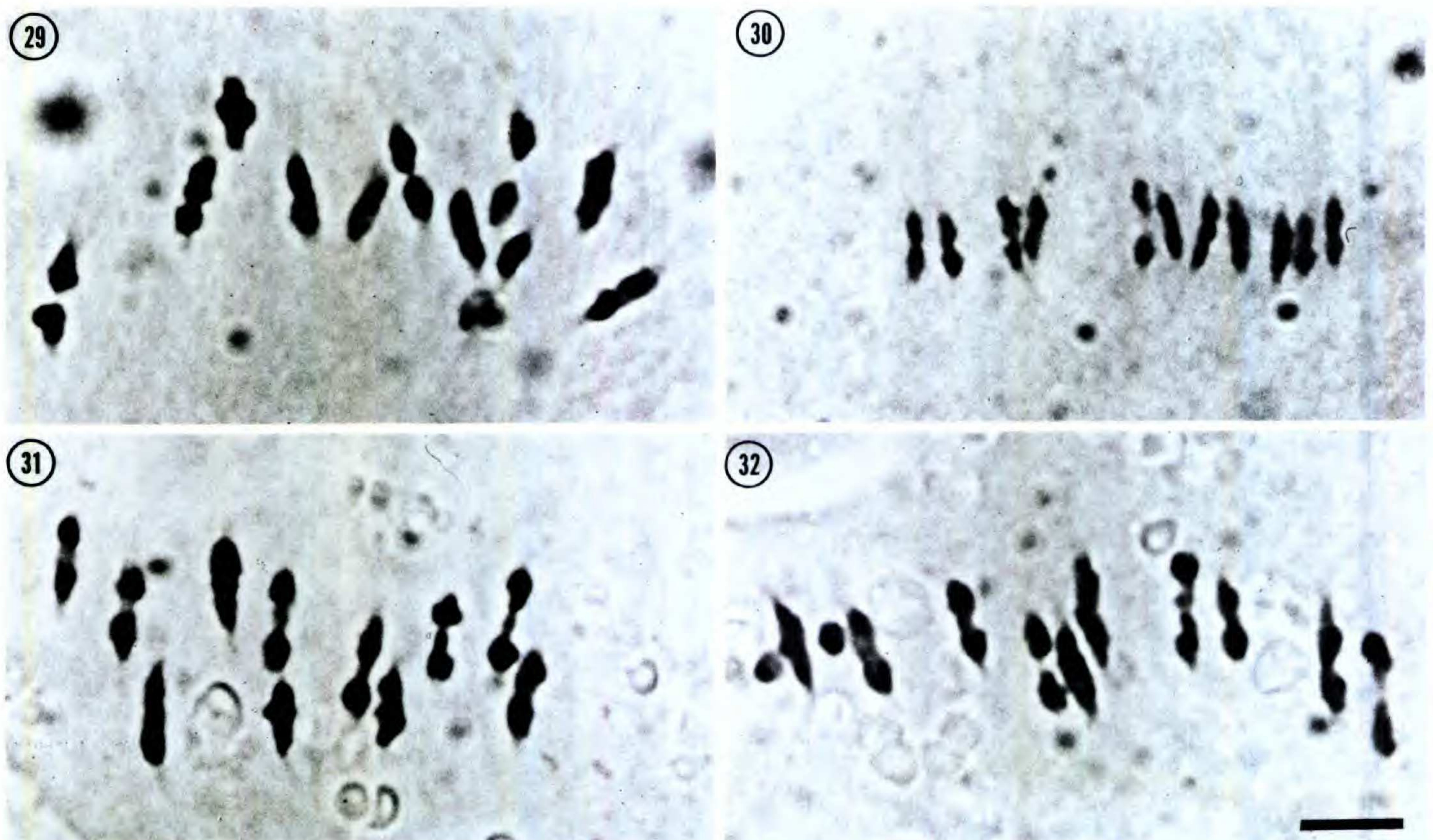
FIGURES 29–32.   Meiotic chromosomes in *Fuchsia cyrtandroides* and in hybrids between *F. procumbens* and *F. excorticata* and *F. perscandens*. Scale bar = 5 µ; photographs by E. J. Beuzenberg.—29. Meiosis in *F. cyrtandroides*, with 11 bivalents, from accession #G9804/6 at D.S.I.R., Lincoln, New Zealand.—30. Meiosis in an hermaphrodite plant of *Fuchsia procumbens* × *F. perscandens*, showing 11 bivalents, from cross 1969/2, plant G8968.—31. Meiosis in a plant of *Fuchsia procumbens* × *F. excorticata*, showing 11 bivalents, from cross 1969/1 (Table 5), accession # G9140/30 at D.S.I.R., Lincoln, New Zealand.—32. Meiosis in a plant of *Fuchsia procumbens* × *F. excorticata*, showing 10 bivalents and 2 univalents, from cross 1969/1 (Table 5), accession # G9140/30 at D.S.I.R., Lincoln, New Zealand.

Table 5. Artificial crosses between South Pacific species of *Fuchsia*.

Cross	Date	Parents (female first)	Number of flowers pollinated	Number of fruit set	Fruit length (mm)	Seeds per fruit	Seeds germinated/sown	Voucher specimens
1951/6	10 Nov.	*F. procumbens* (female) × *F. excorticata* (hermaphrodite)	7	6	9–10	20–41	69/177	CHR 79041 CHR 191429–30 CHR 191432–33
1951/11	19 Dec.	*F. procumbens* (hermaphrodite-male) × *F. excorticata* (hermaphrodite)	5	4	20–27	27–55	2/155	
1952/1	29 Jan.	*F. excorticata* (female) × *F. procumbens* (hermaphrodite-male)	2	1	?	104	3/104	
1969/1	15, 16, 20 Oct.	*F. procumbens* (female) × *F. excorticata* (hermaphrodite)	15	7	10–20	23–65	208/357	CHR 191308–12 CHR 365025 CHR 465324
1969/2	3, 4, 11 Nov.	*F. procumbens* (female) × *F. perscandens* (hermaphrodite)	16	15	10–16	13–49	223/294 + 207[1]	
1969/3	4, 5, 11 Nov.	*F. excorticata* (female) × *F. perscandens* (hermaphrodite)	16	1	10	76	42/76	
1970/1	24 Mar.	*F. ×colensoi* (hermaphrodite) self-pollinated					76/242	CHR 325596 A–D
1973/1	26 Feb.	*F. cyrtandroides* × *F. procumbens* (male)	4	2		273–289	0/562	
1973/2	11 Sep.	*F. perscandens* (hermaphrodite) × *F. cyrtandroides*	1	1		152	N.A.[2]/152	CHR 465323 A–C
1990/1	7 Nov.	*F. excorticata* (female) × *F. perscandens* (hermaphrodite)	3	2			2/(1 fruit)	CHR 484724
1991/1	8 Nov.	*F. excorticata* (female) × *F. perscandens* (hermaphrodite)	10	10	11–13		numerous/350 (5 fruits)	CHR 484725

[1] The second group of seeds was separated before being sown as being malformed and unlikely to germinate; see text for additional discussion.
[2] Number not recorded, but some seed did germinate and grew to flowering stage.
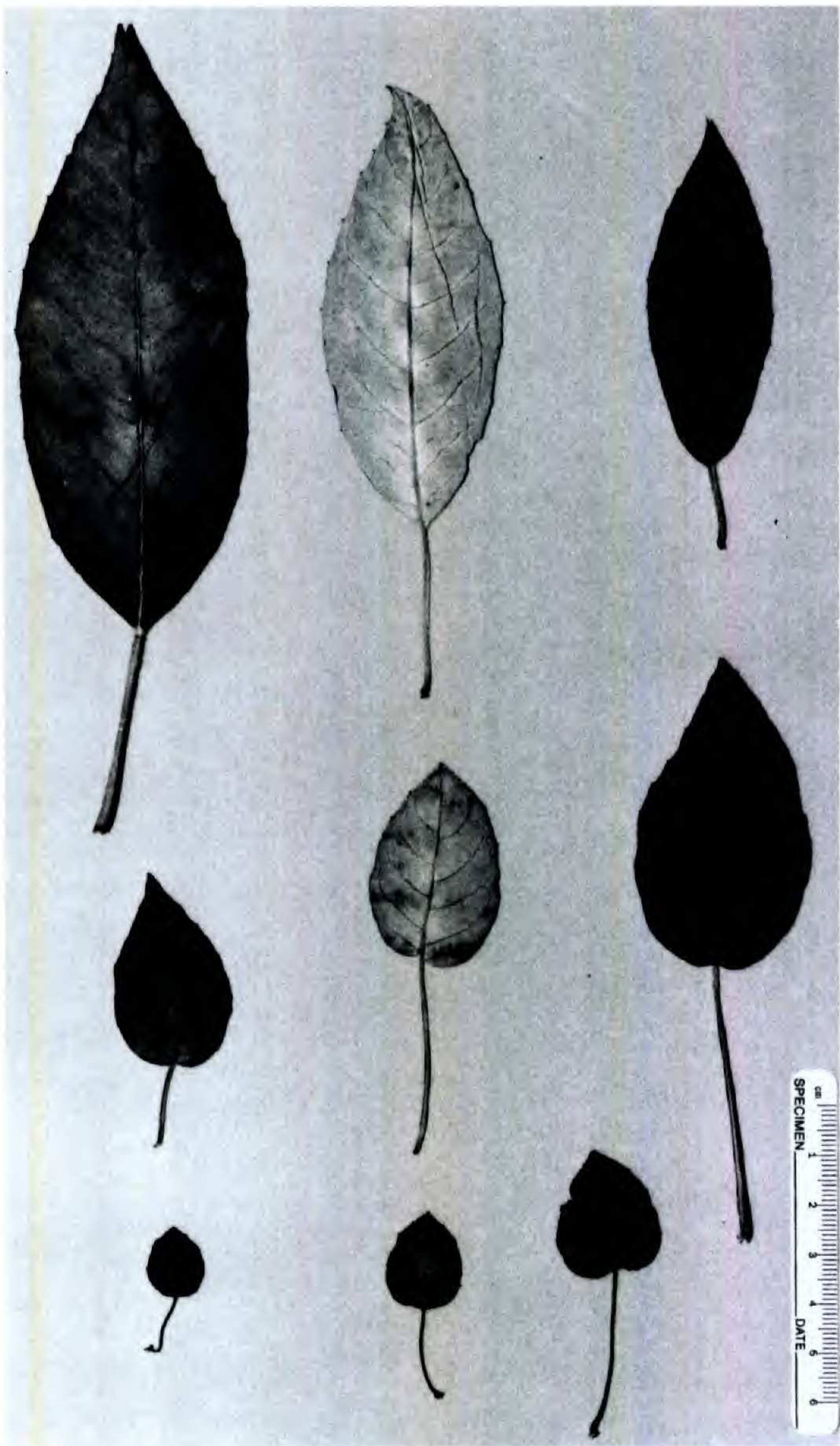
FIGURE 33. Leaves of cross 1990/1 (Table 5) between *Fuchsia excorticata* and *F. perscandens*, showing the range of leaf sizes for the two parents and the F1 hybrids. Top row, *F. excorticata*; middle row, *F. excorticata* × *F. perscandens*; bottom row, *F. perscandens*.

with coarse sand (letter to E. Godley, 16 Feb. 1972).

Allan (1961) wrote that "the species [*F. colensoi*] is maintained meantime, as many of the localities are far outside the known occurrences of *F. perscandens*." His main reason for this statement is that he accepted Cheeseman's (1906, 1925) record of *F. colensoi* from the Northern Wairoa, North Auckland. However, Cheeseman's specimen was actually *F. perscandens*, which was not recognized in his time.

Plants intermediate between *F. excorticata* and *F. perscandens* were first classified as *F. colensoi* Hook. f. Later, Allan (1927) described them as *F. ×experscandens* and wrote, "Where we have found this species [*F. perscandens*] we have observed it to hybridize with *F. excorticata* if that is also present. A polymorphic swarm is produced, many of the

forms of which—their origin being unknown—might be referred to *F. colensoi*. Whether one or more shrubby jordanons exist, or whether *F. colensoi* is purely a series of hybrid forms remains to be investigated." But Allan's alternatives are not mutually exclusive. Both crossing and selfing could be at work. That plants referable to *F. colensoi* can arise as hybrids is shown by our artificial crosses. The hybrids are all hermaphrodite if both parents are hermaphrodite, or if the cross is between an hermaphrodite and a female the progeny will be a mixture of these types. There are opportunities therefore in the F_1 generation for outcrossing and for selfing, the former contributing to polymorphic forms, the latter to more inbred lines.

Field and experimental evidence shows that *F. colensoi* should not be maintained as a species, but that it arises as a fertile natural hybrid between *F. perscandens* and *F. excorticata*. Backcrosses with both parents appear to occur frequently, although *F. ×colensoi* is much more common and widespread than *F. perscandens*. From historical records, it appears that *F. perscandens* was much more common until colonization and deforestation over the last centuries led to the demise of the mainly lowland forested habitats preferred by this species. As a mostly self-supporting bush to a small tree, *F. ×colensoi* is apparently much better suited to disturbed habitats than is *F. perscandens*, and this may help explain why it is currently more common and widespread. Wilson (1982, 1987) reported *F. ×colensoi* from Stewart Island, where *F. excorticata* is known to grow but *F. perscandens* is not; he suggested that birds could have transported seeds of hybrid plants from the mainland.

Cross 1970/1 involved self-pollinated flowers of *Fuchsia ×colensoi* (hermaphrodite) collected on the Otago Peninsula by P. Raven (*Raven 25113*, MO). From 242 seeds 76 plants were reared. Leaf blade dimensions showed little variation and ranged in size from 26 × 20 mm to 56 × 36 mm (leaf samples were taken and mounted as *CHR 325596 A–D*). The smallest leaf approached the presumed *F. perscandens* parent, while most of the plants come within the range of *F. ×colensoi*, and none approached the normal dimensions of *F. excorticata* (see Fig. 33).

A chloroplast DNA restriction site analysis that included samples of *F. excorticata*, *F. perscandens*, and *F. ×colensoi* (Sytsma et al., 1991) remarkably found no differences in the chloroplast genome among the three, which suggests a high level of introgression. It is possible that the maternal genome of the more widespread *F. excorticata* has swamped out that of the much rarer *F. perscandens*.

EVOLUTION AND BIOGEOGRAPHY

The South Pacific species of *Fuchsia* are key elements to understanding evolution in the genus because of their unusual combination of characters and their widely disjunct distribution. Several distinct lines of evidence support the early separation of the South Pacific species from the American fuchsias. Sections *Procumbentes* (see below) and *Skinnera* are the only sections in which all species have flavones, and all of the South Pacific species except for *F. cyrtandroides* have flavone sulphates that occur nowhere else in the genus. Furthermore, these are the only two sections known to have male sterility controlled by a dominant gene, and all four species share the apomorphy of blue pollen. Other distinguishing characters of the South Pacific fuchsias are the greenish flowers and marked floral color changes during anthesis (all three species of section *Skinnera*), the strongly reduced or missing petals, and the wide variety of habit types from trees to small creepers. Chloroplast DNA restriction site analysis of 18 species from ten sections of *Fuchsia* indicated that among those lineages that have persisted until the present, sections *Procumbentes* and *Skinnera* were the first ones to diverge within the genus and that together they form the sister group to all other *Fuchsia* sections (Sytsma & Smith, 1988, 1992).

Fossil pollen records of *Fuchsia* from Oligocene deposits in Australia (Berry et al., 1990), New Zealand (Pocknall & Mildenhall, 1984), and Argentina (E. Romero, pers. comm.), as well as the South American center of distribution for the genus, suggest that *Fuchsia* evolved in subtropical forests of the southern hemisphere during the early to middle Tertiary (Berry et al., 1990). Until the late Eocene or perhaps into the early Oligocene, present-day portions of Australia, Antarctica, and southern South America formed contiguous land masses, with more or less direct overland migrations possible between them (Kennett, 1980; Zinmeister, 1987). Based on the known fossil records of *Fuchsia* in Australia as early as 35 mya, it may be more realistic to estimate the initial diversification of the South Pacific and the New World fuchsias at closer to 50 mya (Sytsma et al., 1991).

Ancestors of the South Pacific fuchsias were likely present in Antarctica and Australia during the Eocene, when both land masses were in close proximity and moist subtropical to temperate forests were the dominant vegetation type. By the Oligocene, *Fuchsia* was already widely scattered in eastern Australia (Berry et al., 1990). Sometime after the mid-Miocene, however, when the last known fossil records are known from Australia, it may have gone extinct there, a victim of increasing warmth and dryness as the continent rafted northwards (Barlow, 1981). New Zealand, on the other hand, has apparently maintained mesic conditions for much of its history since it separated from Australia and Antarctica about 80 mya (Raven, 1979b). Since the oldest fossil grains of *Fuchsia* from New Zealand date from the Late Oligocene, roughly 30 mya (Mildenhall, 1980), it is likely that the genus had to disperse there from Australia across the Tasman Sea, following the prevailing westerlies.

Examination of different kinds of characters in the four South Pacific species of *Fuchsia* does not make their relationships immediately clear. In its tree habit and strongly bicolored leaves, *F. cyrtandroides* from Tahiti is most similar to the New Zealand tree fuchsia, *F. excorticata*. On the other hand, it is the only species in the group with opposite leaves as an adult and that lacks both flavone sulphates and male sterility. Since Tahiti is a young volcanic island approximately 2 MY old (Dymond, 1975), *Fuchsia* either arrived there recently via long-distance dispersal from a source such as New Zealand, as postulated by Carlquist (1967) and others (Raven, 1979a; Fleming, 1976; Godley, 1979; Berry, 1982), or was present on older islands in the Pacific that have since subsided. *Fuchsia procumbens* from New Zealand is the most distinctive species of the group, although it most closely resembles *F. perscandens* vegetatively. *Fuchsia perscandens* has flowers very similar to *F. excorticata*, but differs markedly in its bushy or lianoid habit.

Williams & Garnock-Jones (1986) attempted the first phylogenetic analysis of the South Pacific species, using mostly leaf flavonoids with some habit and flower characters. Their results produced a single, shortest cladogram (Fig. 34A) in which *F. cyrtandroides* was the sister group of the New Zealand species, and *F. excorticata* the sister species of the pair *F. procumbens* and *F. perscandens*. Crisci & Berry (1990) reanalyzed the same taxa with a

→

FIGURE 34. Published trees of the South Pacific species of *Fuchsia* derived from cladistic analysis of morphology and flavonoids.—A. The single most parsimonious tree obtained by Williams & Garnock-Jones (1986).—B, C. The two most parsimonious trees obtained by Crisci & Berry (1990). Note that the tree in B has the same topology as that of A. Reprinted with permission of *Systematic Botany*.
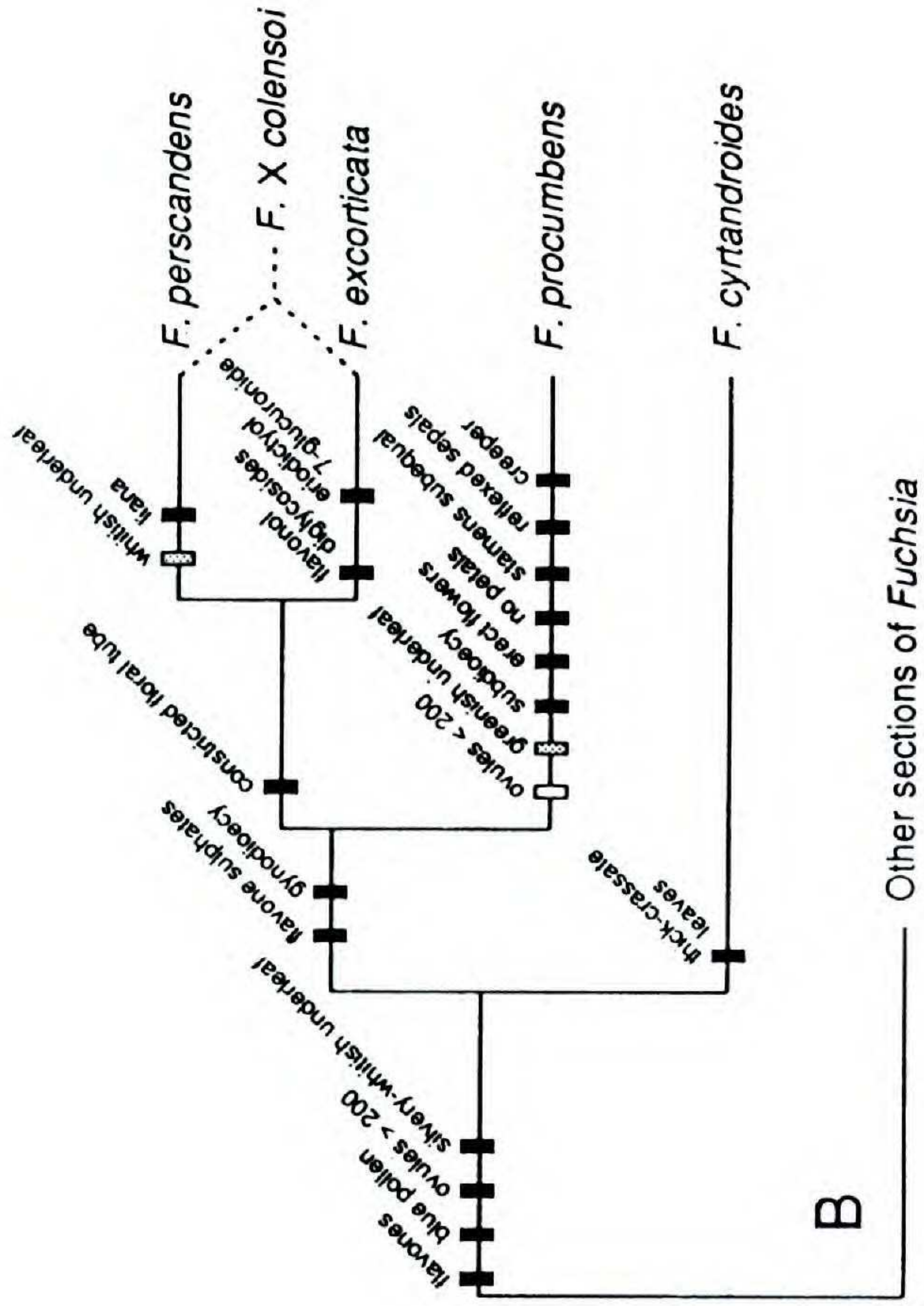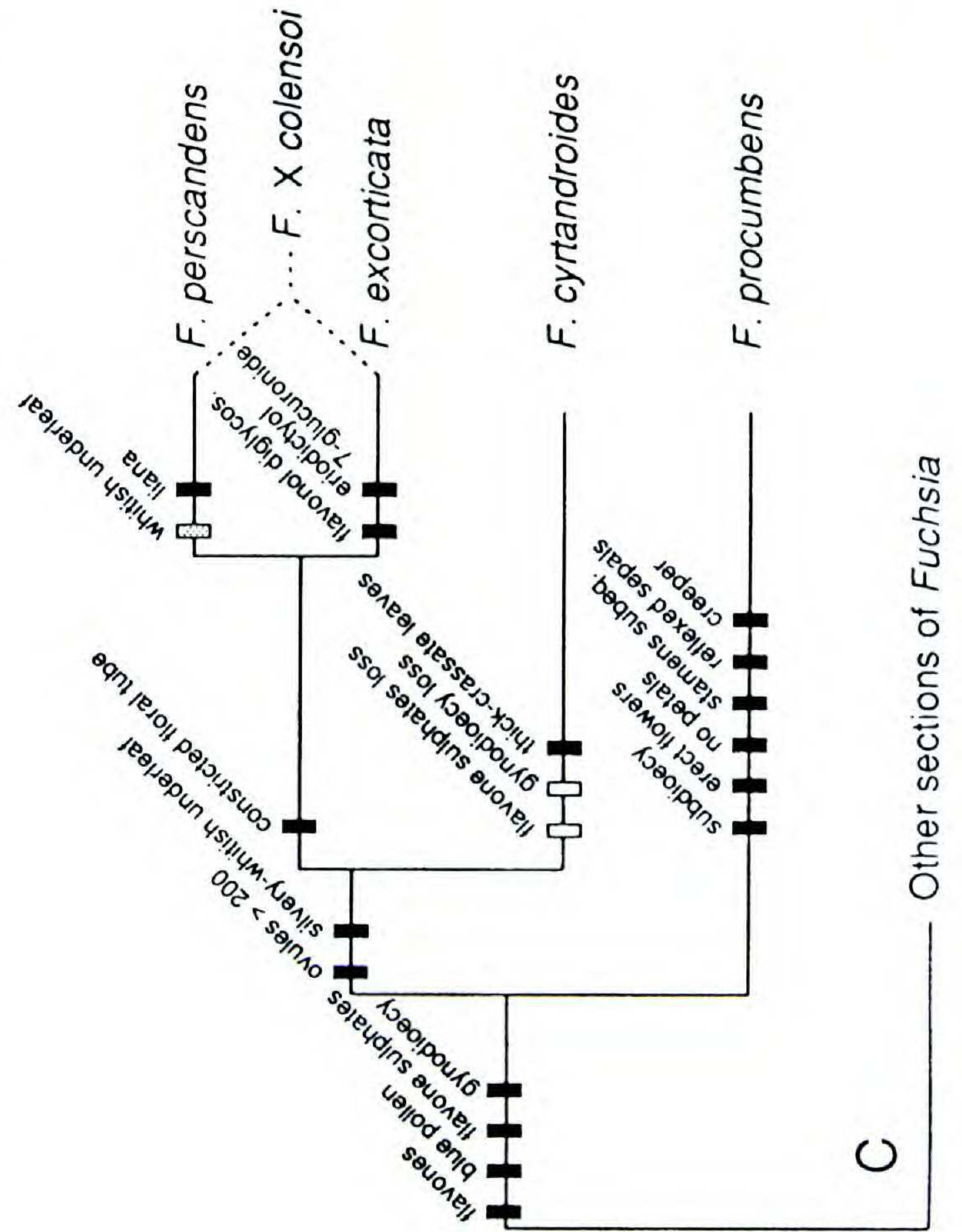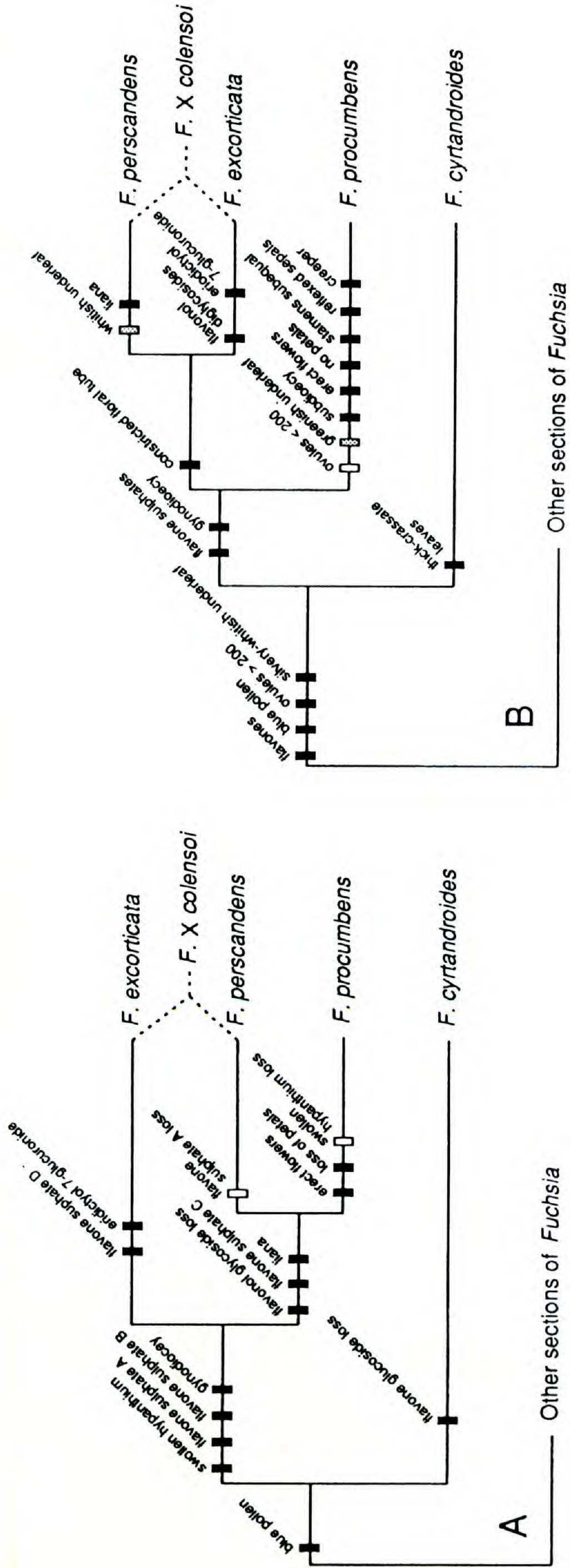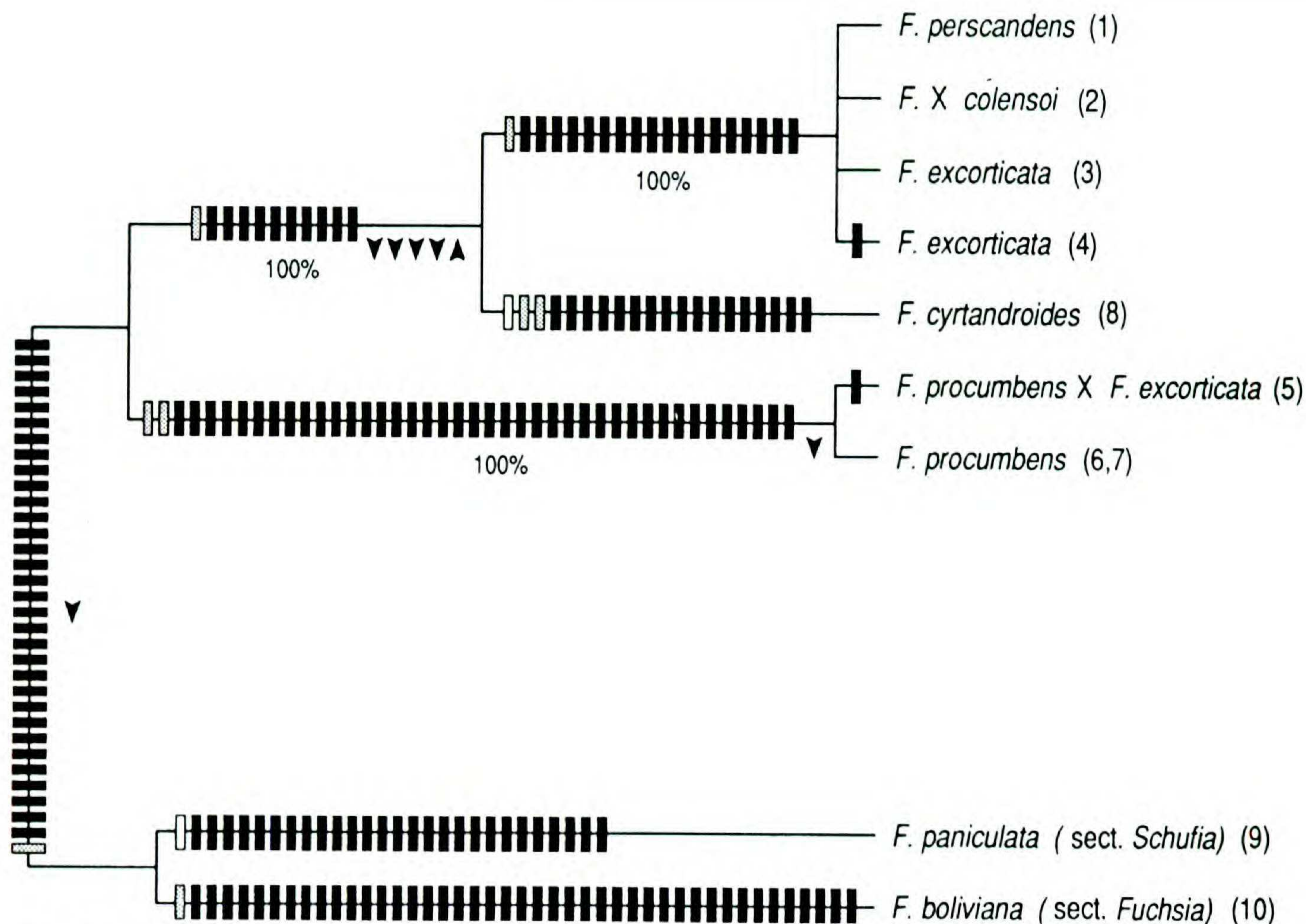
FIGURE 35. The most parsimonious cladogram of the South Pacific species of *Fuchsia* obtained by Sytsma et al. (1991) from chloroplast DNA restriction site mutations. Solid bars represent uniquely occurring site changes. Gray bars represent likely homoplastic site changes (convergent losses, or gains followed by losses), and open bars represent unlikely changes (convergent gains, or losses followed by gains). Downward arrows represent deletions and the upward arrow an insertion (these were not used to generate the tree). For the resolved branches confidence levels are 100% by Wagner bootstrap analysis. Reprinted with permission of *Systematic Botany*.

broader interpretation of flavonoid characters and additional characters from leaves and sexual systems. They arrived at two equally parsimonious trees, both differing from the previous study by placing *F. perscandens* closest to *F. excorticata* rather than to *F. procumbens*. The first cladogram (Fig. 34B) resembled Williams and Garnock-Jones's results in placing *F. cyrtandroides* as the sister species of the other three, while in the second (Fig. 34C), *F. procumbens* was the sister group of the other taxa, with *F. cyrtandroides* the sister species of *F. excorticata* and *F. perscandens*. These differing cladograms were largely the result of the difficulty in polarizing characters such as the presence/absence of flavone sulphates and male sterility.

Sytsma et al. (1991) employed the technique of chloroplast DNA restriction site analysis to examine the four South Pacific species of *Fuchsia*, two interspecific hybrids in this group, and two outgroup species from other sections of the genus. Their phylogenetic analysis of the results of over 790 restriction sites examined within each accession produced a single, highly reliable, and statis-

tically significant cladogram (Fig. 35) that agreed with the second tree of Crisci & Berry (1990, Fig. 34C above), in which *F. procumbens* is the sister group to the other South Pacific species, and *F. cyrtandroides* is the sister group of *F. excorticata* and *F. perscandens*. The chloroplast genomes of *F. excorticata* and *F. perscandens* were virtually indistinguishable, arguing for either a very close relationship between the two or else the swamping of the maternal genome of one species by hybridization and unidirectional backcrossing to the other.

This robust phylogenetic tree of the South Pacific *Fuchsia* species from detailed molecular data supports an early divergence of *Fuchsia procumbens* from the other South Pacific species. This lends strong support to the recognition of a new section *Procumbentes* to accommodate *F. procumbens* as the sister group to the three species of section *Skinnera*. A relatively ancient separation of these two South Pacific lineages is consistent with the early presence of *Fuchsia* fossils in New Zealand and Australia. Within section *Skinnera*, the large number of differences in cpDNA between *F. cyrtan-*

droides and the *F. excorticata–F. perscandens* species pair suggests that these two clades diverged about 10 mya, long before Tahiti emerged from the Pacific ca. 2 mya (Sytsma et al., 1991). One explanation is that *F. cyrtandroides* or its immediate ancestor evolved for a considerable amount of time in New Zealand or on another island, then became extinct there after dispersing to Tahiti or older, now submerged islands in the mid-Pacific.

The study by Sytsma et al. (1991) also has important implications for character evolution in the South Pacific sections. When the morphological, flavonoid, and sexual characters are superimposed on the molecular-derived cladogram, gynodioecy appears as the ancestral condition to all South Pacific species, with *F. procumbens* becoming subdioecious through the subsequent development of female sterility, and *F. cyrtandroides* becoming hermaphroditic through the secondary loss of male sterility. Likewise, the absence of flavone sulphates in *F. cyrtandroides* must be viewed as a secondary loss, rather than a primitive absence shared with the New World species. Lastly, the shrub or tree habit in *F. cyrtandroides* and *F. excorticata* should not be interpreted as a shared, derived character, but rather as the generalized condition in the genus. The unusual, procumbent habit of *F. procumbens* and the lianoid habit of *F. perscandens*, on the other hand, are best viewed as independently derived conditions from shrubby ancestors.

The progression of studies outlined above dramatically illustrates the perils of making conclusions about biogeography and character evolution without an exhaustive analysis of several kinds of evidence, including molecular studies. There is already evidence for extensive homoplasy in *Fuchsia* in characters such as leaf position, nectary types, breeding systems, floral color changes, loss of petals, polyploidy, and pollen morphology and ultrastructure. For these reasons, considerable caution will be needed in interpreting relationships and phylogenetic trends in the other parts of the genus.

TAXONOMIC SECTION

Because of the distinctiveness of *Fuchsia procumbens* and its basal position within the South Pacific clade, we choose to recognize it as a new section. It is distinguished morphologically by a very different fruit type from section *Skinnera*, the absence of petals, erect flowers that do not undergo marked changes in flower color during anthesis, and a unique habit type in the genus. These are characters that would readily be recognized at the sectional level for any of the American species. The

ease of hybridization between *F. procumbens* and members of section *Skinnera* is not a strong argument to maintain them as a single section, as it is easy to produce intersectional hybrids between many of the American sections, and members of both section *Skinnera* and *Procumbentes* have successfully produced hybrid progeny when crossed with American species in the greenhouse.

KEY TO THE SOUTH PACIFIC TAXA OF *FUCHSIA*

1. Flowers erect, without petals; procumbent subshrubs (section *Procumbentes*) _____ 1. *F. procumbens*
1. Flowers pendulous, with small, lanceolate petals; trees, shrubs or lianas (section *Skinnera*) _____ 2
2. Plant a liana or densely branched, scandent to compact shrub; leaves suborbicular to broadly ovate, pale green below, secondary veins 3–5 per side, petiole ½ to 1 times the blade length _____ 4. *F. perscandens*
2. Plant a tree or erect to sometimes scandent shrub; leaves elliptic-ovate to lanceolate, whitish to silvery below, secondary veins 6–12 per side, petiole mostly less than ½ the blade length _____ 3
3. Floral tube cylindrical, the base not bulbous; leaves mostly opposite, the apex rounded or obtuse; Tahiti _____ 2. *F. cyrtandroides*
3. Floral tube strongly constricted in the middle, the base bulbous; leaves mostly alternate, the apex acute to acuminate; New Zealand _____ 4
4. Plant a tree with distinct trunk; leaves mostly > 5 cm long, secondary veins 9–12 per side _____ 3. *F. excorticata*
4. Plant a shrub, much branched from the base, branches often scandent; leaves mostly < 5 cm long, secondary veins 6–8(9) per side _____ 5. *F. ×colensoi*

Fuchsia section Procumbentes E. J. Godley & P. E. Berry, sect. nov. TYPE: *Fuchsia procumbens* R. Cunningham ex A. Cunningham.

Sectioni *Skinnerae* affinis, a qua differt habitu subligneo serpentique, floribus erectis subdioeciis, sepalis reflexis, petalis nullis, staminibus fere uniseriatis, ovario 50–230-ovulato, fructus loculis cavis.

Trailing subshrubs. Leaves alternate, suborbicular to broadly ovate, firmly membranous, weakly bicolored, sinuate- or serrulate-margined, the blade shorter than the petiole. Subdioecious (plants male, female, or sometimes male-hermaphrodite), the flowers axillary and erect, females smaller than males or male-hermaphrodites. Floral tube cylindrical, light green in bud, pale orange-yellow at anthesis; nectary a smooth band lining the inner, basal part of the tube. Sepals completely reflexed soon after anthesis. Petals absent. Stamens uniseriate or weakly biseriate; pollen bright blue, 2-aperturate, with beaded to nearly smooth viscin threads. Stigma capitate and somewhat 4-angled when functional. Ovary green, with 50–230 biseriate ovules.

Berry ovoid-oblong to subglobose, 10–25 × 8–16 mm, bright red with a pruinous covering when ripe, firm-walled, with hollow locules; seeds oblong to (ob-)ovoid, 1.7–2.8 mm long, 1.3–1.6 mm wide. Gametic chromosome number $n = 11$.

Distribution (Fig. 6). Far northern districts of the North Island of New Zealand.

1. **Fuchsia procumbens** R. Cunningham ex A. Cunningham, Ann. Nat. Hist. 3: 31. 1839. TYPE: New Zealand. North Island: around the village of Matauri, on the E coast opposite the Cavallos Isles, inhabiting the sands immediately above the range of the tide, Mar. 1834, (female), *Richard Cunningham* (holotype, K).

Fuchsia kirkii Hooker f., Icon. Pl. 11: 66, pl. 1083. 1871. TYPE: New Zealand. Great Barrier Island: near the sea, Dec. 1867, (male), *Thomas Kirk 62* (holotype, K).

Densely branched, procumbent subshrubs, with slender, trailing main stems 1–2(–8) mm thick, to 2 m long, often rooting along the ground and with exfoliating bark when old; young branchlets very slender and glabrous, ascending near the tips, sometimes scandent on tree trunks or in dense brush. Leaves alternate, firm-membranous, suborbicular to broadly ovate, 5–28 mm long, 3–27 mm wide, apex obtuse to rounded, base subcordate to truncate, pale green to purple-flushed on both surfaces, slightly paler beneath; margin sinuate to serrulate with prominent glandular teeth, strigulose along the nerves, secondary veins (3)4 or 5(6) per side, lower order venation inconspicuous. Petioles slender, strigulose, longer than the blade, 5–50 mm long. Stipules minute, narrowly lanceolate, 0.3–0.9 mm long, ca. 0.2 mm wide at the base, caducous.

Subdioecious; flowers axillary and erect on pedicels 3–10 mm high. *Staminate or perfect flowers:* ovary cylindrical, 3–6 mm long, 2–2.8 mm thick, green and pruinous, 4-locular, each locule with 15–55 ± biseriate ovules. Floral tube cylindrical, 7–11 mm long, 5.2–7.5 mm wide at the rim, light green in bud, pale orange-yellow at anthesis, in some cases turning slightly darker with age; nectary 2–4 mm high, lustrous yellow-orange. Sepals lanceolate, acute, 7–9 mm long, 2.7–3.8 mm wide at the base, completely reflexed soon after anthesis, light to dark purple on the exposed, inner surface except at the green base, green on the hidden, outer side. Petals absent. Filaments equal or subequal, 3.5–5 mm and 3.2–4.5 mm long, pink to red or yellow near base; anthers oblong, dorsifixed, 1.5–2.4 mm long, 1–1.5 mm wide, purple. Style included or exserted beyond the tube, 6–9(–14) mm long,

pale pink; stigma capitate, 0.4–1 mm thick, yellow-green or dull brown, or style acephalous and stigma non-functional. *Pistillate flowers* similar to staminate flowers, except: ovary 5–8 mm long. Floral tube 5.5–9 mm long, 3.8–5.4 mm wide at the rim. Sepals 4.1–6.4 mm long, 2.2–2.8 mm wide at the base. Filaments 1.6–2.7 mm and 1.6–2.4 mm long, red-purple; anthers sterile, 0.85–1.05 mm long, 0.4–0.7 mm wide, pink. Style exserted, 7–15 mm long; stigma capitate and 4-angled, 1.1–2.2 mm long, 1.8–2.5 mm wide, yellow-green; ovules 50–230 per ovary, biseriate in each locule. Berry ovoid-oblong to obovoid or subglobose, somewhat 4-angled, 10–25 mm long, 8–16 mm wide, bright red to magenta when ripe with a light purple, pruinous wax, fruiting pedicel 5–23 mm long; ovary wall firm, not becoming juicy or succulent at maturity, locules hollow; seeds tan, biseriate, oblong to (ob-) ovoid, 1.7–2.8 mm long, 1.3–1.6 mm thick, rugulose, usually between 20 and 80 per fruit. Gametic chromosome number $n = 11$.

Distribution (Fig. 6). A scarce plant in small populations along the far northern coast of the North Island of New Zealand, often associated with *Metrosideros excelsa* coastal forests or growing among *Phormium tenax* (flax) or *Cyperus ustulatus*. From North Cape to Maunganui Bluff on the west coast and to northern Coromandel Peninsula on the east coast, sea level to 150 m; flowering from October to March.

Representative specimens examined. NEW ZEALAND. **North Auckland:** North Cape District, 1896, (female), *Adams s.n.* (AK); Spirits Bay, Northland, Dec. 1926, (female), *Carse 982/A* (CHR); Kerr Point, 100 ft., 1 Sep. 1964, *G. K. R. & W. D. Burke s.n.* (WELTU); Scott Point, North Cape, Jan. 1913, *H. B. Matthews & Carse 982/4* (CHR); Houhora, base of Mount Camel at Cape Perpendicular, 6 Jan. 1952, (hermaphroditic-male), *Godley G2207* (CHR); Waihi, 20 mi. N of Ahipara, Jan. 1896, (male, reduced style), *Cheeseman s.n.* (AK, 2 sheets; WELT); near Reef Point, West Coast, Mangonui Co., Jan. 1901, *R. H. Matthews*, The Carse Herbarium No. 982/1 (CHR); Waipoua State Forest, Hokianga Co., 31 May 1983 (fr), *Wright 5600* (AK), 23 Feb. 1985, (male), *Wright 7094* (AK); S end of Maunganui Bluff, West Coast, growing among flax, 30 Nov. 1981, ("mainly male, few hermaphrodite"), *Lloyd s.n.* (CHR); Whangaroa, *Kirk s.n.* (WELT); Butterfly Bay, next to Tauranga Bay, in Whangaroa Bay, with *Ipomoea palmata*, 27 Mar. 1971, *Rawlings s.n.* (CHR); around the village of Matauri, on the East Coast, opposite the Cavallos Isles, inhabiting the sands immediately above the range of the tide, Mar. 1834, (female), *R. Cunningham* (K); Matauri Bay, 11 Dec. 1950, (male), *Godley G2203* (CHR, 2 sheets); Bay of Islands, Poraenui Point, with gorse and sheep under pohutukawa, 8 Nov. 1970, (male), *Rawlings s.n.* (CHR); Lizard Bay, Deep Water Cove, Bay of Islands, 16 Jan. 1970 (fr), *Engelhorn 25719* (CHR, 3 sheets), *25720* (CHR), Jan. 1965, (female), *Reynolds 155441* (CHR); Whangaruru, 18 Oct.

1969, (male), *Raven 25147* (CHR); Ngawae, 30 Dec. 1950, (female), *Godley G2206* (CHR, 2 sheets); Ngawae, Helena Bay area, 18 Oct. 1969, (male), *Raven 25145* (CHR); Ngahau Bay, Whangarei Co., Oct. 1946, (male), *Olsen N16/90–31* (AK); Matapouri, Dec. 1950, (male), *Godley G2209* (CHR, 2 sheets); Pataua River, Whangarei, Dec. 1876 (male), *Cheeseman s.n.* (AK); Bream Head, Whangarei, on shore of Peach Cove, 23 May 1979, *Ogle 96* (CHR). **Great Barrier Island:** Mine Bay, 21 Nov. 1950, *Trevarthen s.n.* (AK); Rangiwhakaea Bay, banks of Slip Stream, 1 Jan. 1983, (female), *Wright 5332* (AK); Whangaparapara Harbour to right of wharf, Nov. 1950, (female), *R. Lloyd 71615* (CHR); Tryphena Bay, 11 Dec. 1867, (male), *Kirk s.n.* (WELT 24809 and 24837); Johnson's Bay, directly S of Ruahine Trig., Apr. 1980, *Ogle 387* (CHR). **Coromandel Peninsula:** Cape Colville, Mellsop's Beach, 11 Dec. 1929, (female), *Moore 22139* (CHR); near Cabbage Bay, *Adams s.n.* (WELT); Rabart's Road, Tuateawa, 18 Oct. 1982, (male), *Smith-Dodsworth s.n.* (AK); Kennedy Bay, ca. 2 mi. along shore from N head of harbour, Jan. 1977, (male), *Bartlett N.40* (CHR).

In the summer of 1867 to 1868, Thomas Kirk collected at Great Barrier Island (Hamlin, 1965), where he gathered a procumbent plant which he "doubtfully" described as a variety of *F. procumbens* (Kirk, 1869: 147). However, duplicate material sent to Kew was described by Hooker (1871) as a new species, *F. kirkii*, based on differences in floral dimensions from *F. procumbens*. Soon thereafter, Hooker (1874) realized that the differences were due to sexual dimorphism, with *F. kirkii* based on the male morph of *F. procumbens*, and *F. procumbens* itself based on a female plant. In 1875, a second edition of volume 1 of the *Transactions and Proceedings of the New Zealand Institute* was printed (the original edition was printed in 1869). This second edition was paginated differently from the first one, so that Kirk's statement about the new variety of *F. procumbens* was on page 92 (Kirk, 1875). In this second edition, Kirk added the new name *F. kirkii* Hook. f. to the article, not yet aware that Hooker had changed his mind. This modified reprinting led Munz (1943) to give the following erroneous citation: "*Fuchsia kirkii* Hook. f. ex T. Kirk, Trans. and Proc. New Zealand Inst. 1: 92. 1868." Munz was obviously working from the second edition of Volume 1 and was either unaware that this was the second edition, or assumed that it was identical in content and pagination to the first. As a result, he gave the page number of the second edition (page 92) to the first edition (where it is page 147) and implied that the name *F. kirkii* is present in the first edition, when it is not. He also miscited the date of the first edition as 1868, rather than 1869.

Fuchsia section Skinnera (J. R. & G. Forster) de Candolle, Prodr. 3: 39. 1828. *Skinnera* J. R.

& G. Forster, Char. Gen. Pl. 58, pl. 29. 1776. TYPE: *Fuchsia excorticata* (J. R. & G. Forster) Linnaeus f.

Trees, shrubs, or lianas. Leaves alternate to opposite or rarely ternate, membranous to coriaceous, entire to sinuate or serrulate, weakly to strongly bicolored, light green to white or silvery on lower surface, the blade subequal to or longer than the petiole. Hermaphroditic or gynodioecious; flowers axillary and solitary, pendulous or divergent, sometimes grouped on shortened side shoots, females smaller than hermaphrodites. Floral tube cylindrical or obconical with a sharp constriction above a bulbous base, green in bud, initially green at anthesis but then changing to red or purple in late anthesis; nectary a smooth band lining the inner, basal part of the tube. Sepals spreading or recurved. Petals lanceolate, erect, 1.2–11 mm long, purple. Stamens biseriate, the antesepalous stamens longer than the antepetalous ones; pollen bright blue, 2-aperturate, with beaded to nearly smooth viscin threads. Stigma capitate to quadrangular, slightly 4-lobed when functional. Ovary with ca. 500–700 multiseriate ovules. Berry oblong, 5–16 mm long, red to deep purple, fleshy; seeds oblong-triangular to oblong, 0.75–1.2 mm long, 0.3–0.6 mm wide. Gametic chromosome number $n = 11$.

Distribution (Figs. 5 and 6). New Zealand and Tahiti (Society Islands).

2. **Fuchsia cyrtandroides** J. W. Moore, Occas. Pap. Bernice Pauahi Bishop Mus. 16(1): 13, fig. 8. 1940. TYPE: French Polynesia. Society Islands: Tahiti, S side of Mount Orohena, rainforest, 1500 m, occasional tree 5 m high, 15 cm diam., 14 May 1927, *L. H. MacDaniels 1315* (holotype, BH, photograph, POM; isotype, BISH, fragment at POM 260882). Figure 36.

Small tree (2–)3–7 m tall, with numerous ascending branches; trunk with tan-copper, slightly fissured bark, 5–30 cm diam. Branchlets subglabrous, 4–6 mm thick, usually quadrangular. Leaves mostly opposite, occasionally ternate, less commonly alternate or subopposite, subcoriaceous to firm-fleshy, (broadly) elliptic or obovate, (2–)4–12 cm long, (1.5–)2–6 cm wide, rounded or obtuse at apex, rounded to acute at base, green above, whitish below and sometimes purple-flushed; margin subentire with small, reddish, glandular teeth; midvein raised below, secondary veins (7)8–12 on each side. Petioles stout, 1.5–3 mm thick when fresh, 5–
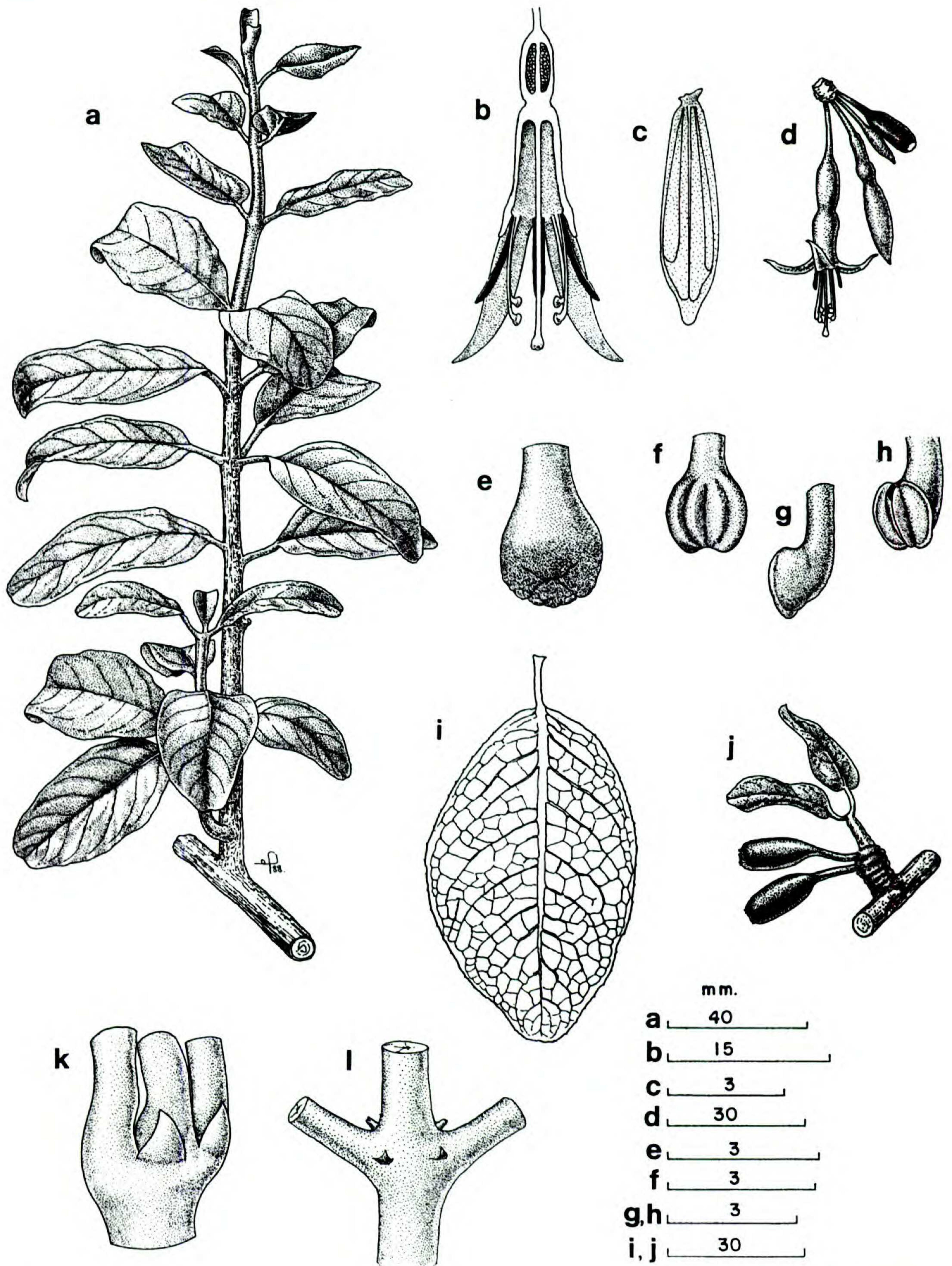
FIGURE 36. *Fuchsia cyrtandroides.*—a. Habit.—b. Longitudinal section through a flower.—c. Petal.—d. Ramiflorous cluster of flowers.—e. Stigma.—f. Anther, before dehiscence, facing toward the central style.—g. Side view of anther.— h. Dehiscent anther.—i. Adult leaf showing venation pattern.—j. Young fruits on a side shoot with young leaves emerging.—k. Young leaf node showing stipules.—l. Older leaf node, as the stem enlarges and the stipules begin to dry out. Drawing by E. Pérez.

25(–35) mm long. Stipules triangular, dark purple, 0.5–0.8 mm long, 0.40–0.75 mm wide and crassate at the base, caducous.

Hermaphroditic; flowers axillary on young, leafy shoots or grouped on short, leafless side shoots off the main branches. Pedicels stout, 5–20 mm long, pendulous in flower, divergent to erect in fruit, with the upper 5 mm enlarged and dark purple. Ovary cylindrical-fusiform, 6–8.5 mm long, 3–4.5 mm thick, green; ovules 500–600, 4- or 5-seriate in each locule. Floral tube cylindrical to slightly fusiform, slightly tetragonous, 6–14 mm long, 5–9 mm wide at the rim; nectary poorly defined, 3–5 mm high. Sepals lanceolate, 7–19 mm long, 3.5–7 mm wide at the base, spreading to recurved. Floral tube and sepals green with dark purple streaks in bud and at anthesis, changing abruptly to dark crimson-purple before dehiscing. Petals oblanceolate to elliptic, 4–11 mm long, 1–4 mm wide, erect, lavender to light purple, turning darker with age. Filaments 0.8–1 mm thick, 6–18 mm and 5–12 mm long, purple; anthers suborbicular, attached apically with a thick connective, 1.3–1.8 mm long, 1.5–2.5 mm wide, purplish, with reniform thecae. Style stout, 1–1.5 mm thick, 14–30 mm long, faint cream-colored to purple; stigma clavate to capitate, 1.5–3 mm long, 1.5–3 mm wide, faintly 4-cleft at apex, light green. Berry oblong-fusiform or ellipsoid, 9–16 mm long, 5–10 mm wide, purple-black and juicy when ripe; seeds oblong-triangular, 0.9–1.2 mm long, 0.4–0.7 mm thick, light brown. Gametic chromosome number $n = 11$.

Distribution (Fig. 5). Endemic to several of the highest peaks on the western (drier) side of the island of Tahiti, from 1150 to 2000 m; flowering mostly in dry season (July–October), but occasionally and less intensively in other months throughout the year.

Specimens examined. FRENCH POLYNESIA. TAHITI. **Mont Marau:** along road to antenna and in adjacent valleys, 1200–1450 m, 4 Feb. 1988, *Berry, Guérin & Florence 4628* (PAP, MO); N flank of Mont Marau, roadside, 1370 m, 24 Mar. 1982, *Florence & Guérin 2713* (PAP, 2 sheets); Haute Tipaerui, sentier *Fuchsia*, 1380 m, 26 July 1983, *Florence 4700* (BISH, K, NY, P, PAP, US), 15 Oct. 1982, *Flynn & Flynn 329* (PAP); highest slopes and ridges around the disturbed summit, 1480–1490 m, 19 July 1981, *Fosberg 61095* (CHR); Mont Marau road, crest between Tapaerui and Punaruu valleys, 1250 m, 5 June 1982, *Fosberg 62646* (CHR); 1 Sep. 1973, *Godley* (CHR); 1400 m, 20 Mar. 1977, *Sachet 2352* (MO, US), 2 Sep. 1980, *Veillon & Guérin 38* (BISH, P, PAP, US). **Mont Aorai:** "Les Grosses Pierres," 4000 ft., 15 June 1962, *Carlquist 653* (DS, 2 sheets, RSA; $n = 11$); summit crests above Fare Ata, Comune de Pirae, 1900 m, 8 Apr. 1986, *Florence 7631* (BISH, K, P, PAP); right side of the high valley of Pirae, below the Aorai path, Comune de Arue,

1405 m, 18 July 1986, *Florence 7748* (PAP); 3 Sep. 1973, *Godley* (CHR); Sentier Aorai, crêtes bord ravin, 1500 m, 10 July 1964, *Maclet 156* (CHR); Aorai, Comune de Mahina, 4000 ft., 5 June 1930, *Grant 3742* (A, BISH, K). **Mont Orohena:** N flank of summit of Mt. Pitohiti, path to Orohena, Comune de Mahina, 2000 m, 19 Oct. 1983, *Florence 5455* (BISH, P, PAP, US); S side of Mont Orohena, 1500 m, 16 May 1927, *MacDaniels 1341* (BISH); S ridge, 1600 m, 22 Sep. 1934, *St. John & Fosberg 17005* (BISH).

3. **Fuchsia perscandens** Cockayne & Allan, Trans. Proc. New Zealand Inst. 57: 53, fig. 1. 1926. TYPE: New Zealand. North Island: Kitchener Park, Feilding, forest margins as liane, Sep. 1926, *H. H. Allan 982a* (lectotype, selected here, CHR 330298; see Fig. 37).

Slender and densely branched, usually decumbent shrub 1–2 m tall, or liana 2–8 m tall with strongly flexuous stems to 5 cm diam. and up to 10 m long; bark brown, flaking off in strips; branchlets strigulose. Leaves alternate, firm-membranous, broadly ovate to suborbicular, 7–40 mm long, 5–33 mm wide, acute to rounded at apex, subcordate to rounded at base, pale green, paler beneath, glabrous to strigulose along the margins and veins; margin remotely serrulate to sinuate; secondary veins 3–5 on either side. Petiole slender-filiform, semi-translucent, 10–40 mm long, subequal to the blade length, strigulose above, the basal 1–1.5 mm swollen and crassate, purple when fresh, tan when dry, generally persistent on the stem after the leaf dehisces. Stipules narrowly triangular, 0.8–1.3 mm long, 0.3–0.6 mm wide, semisucculent and purple when young, caducous.

Gynodioecious. *Perfect flowers*: solitary, sparse; pedicels slender, drooping, 4.5–12.5 mm long. Ovary cylindrical, 3–7 mm long, 1–2.4 mm thick, green. Floral tube 9–16 mm long, 2.2–4 mm wide and bulbous at the base, lined by a smooth nectariferous band inside, sharply constricted above to 1.3–2 mm wide, then widening abruptly to 5.5–7.5 mm wide at the rim, 4-angled in bud. Sepals lanceolate, 7–12 mm long, 3–4.4 mm wide at the base, spreading to occasionally reflexed. Tube and sepals lustrous green at anthesis, with dull purple streaks in upper parts between the ridges of the tube, both changing ± abruptly to red-crimson throughout before dehiscing. Petals dark purple, elliptic, 1.5–4 mm long, 0.6–1 mm wide in the middle, acute or obtuse at apex. Filaments 5.2–11 mm and 4.2–8 mm long, purple, pale cream on connective; anthers 1.6–2.5 mm long, 1–1.7 mm wide, purple. Style 20–36 mm long, pale cream to purple; stigma capitate, 1–1.9 mm long, 0.8–1.1 mm wide, yellow-green. Berry subcylindric, 5–9 mm long, 4–5.5 mm
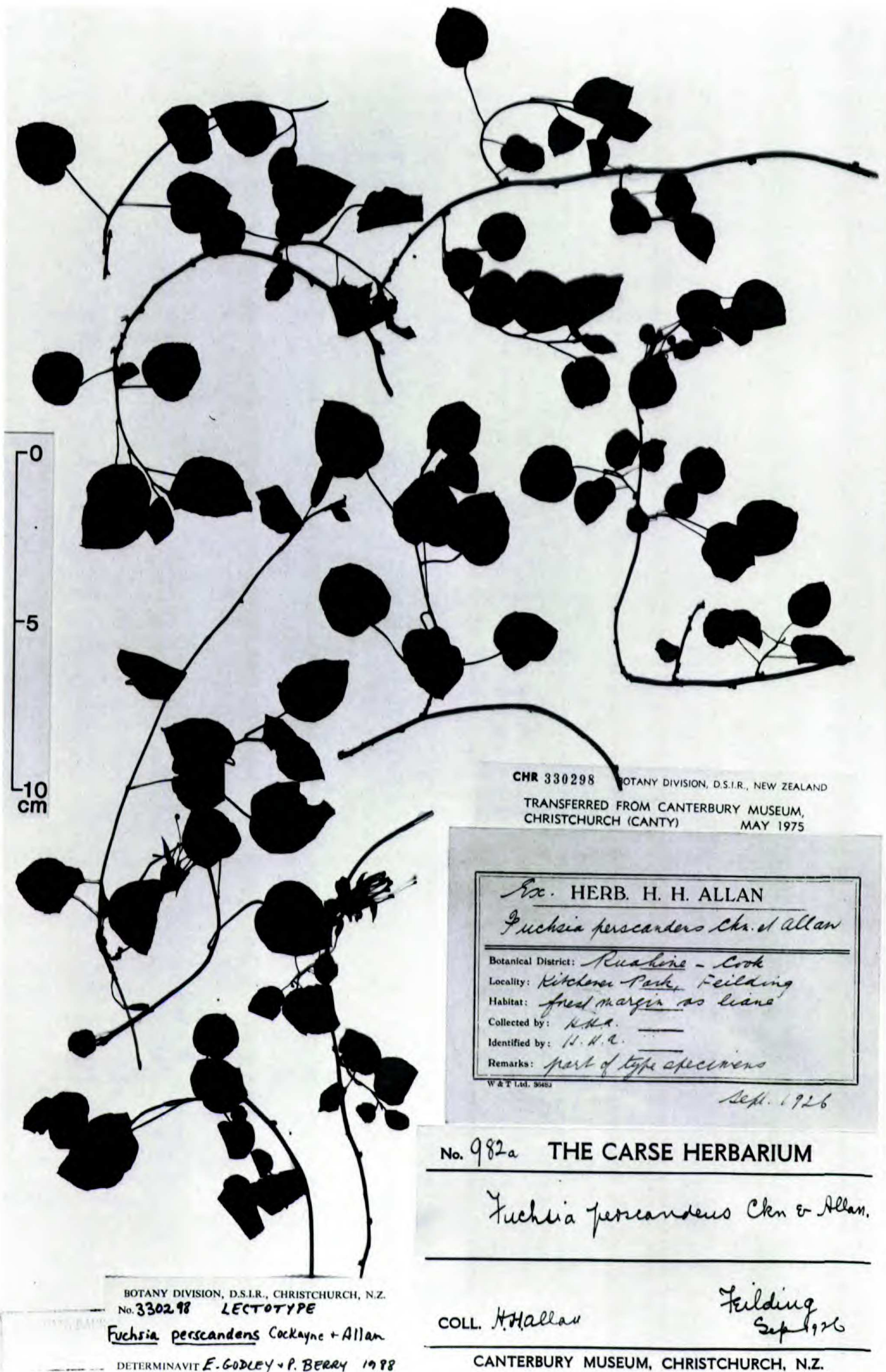
FIGURE 37.   Lectotype of *Fuchsia perscandens*, CHR 330298. Photograph by R. Lamberts.

thick, dark purple when ripe; seeds oblong-triangular, 0.8–1.1 mm long, 0.4–0.6 mm wide. *Pistillate flowers*: similar to perfect ones except: pedicels 4–16 mm long. Floral tube 5.8–10.8 mm long, 1.1–2.5 mm diam. at the constriction, 3.5–5.3 mm wide at rim. Sepals 5.7–9 mm long, 2.6–3.4 mm wide at base. Filaments 2.5–5.2 and 1.5–4.4 mm long; anthers aborted, 0.7–1.1 mm long, 0.5–0.7 mm thick. Style 16–27 mm long; stigma 1–2.2 mm thick. Gametic chromosome number *n* = 11.

Distribution (Fig. 6). New Zealand, infrequent in lowland forests, especially at margins and near clearings, on the North Island as far north as 36°S latitude (historical data), now known no farther north than 37°15′S latitude near Paeroa, and throughout the South Island at scattered localities as far south as Bluff (46°36′S), 0–550 m; flowering from August to March.

Representative specimens examined. NEW ZEALAND. **Northern North Island:** Northern Wairoa, *Cheeseman in Jan. 1875* (AK, 2 sheets); near Whangape Lake, Lower Waikato, *Kirk s.n.* (WELT); Opuatia Creek, Waikato, *Kirk s.n.* (WELT); Whangamarino Swamp, near Kopuku coalmine, *Ogle 563* (CHR), *726* (CHR); 8 mi. NW of Paeroa, *Bartlett TV181* (CHR); Thames River, Te Aroha, *Cheeseman in Jan. 1884* (AK); Hammond Bush, Hamilton City, *de Lange on 4 Dec. 1991* (AK); White Pine Bush, near Whakatane, *Hynes in 23 Dec. 1966* (AK); Otorohanga Co., Awaroa-Mahoenui Valley Road, Awaroa Scenic Reserve, near Te Koraha, *de Lange in 21 Oct. 1984* (AK); Aranui Cave, Waitomo Caverns, *Raven 25192–2* (CHR), *25192–4* (CHR); Waitomo Co., Mangapu Stream, 5 km NW of Te Kuiti, *Gardner 3142* (AK, WELT). **Central North Island:** Taumarunui, *Davidson & Petrie in Nov. 1908* (WELT); Taumarumi Co., Kouturoa Stream, 2 km S of Kaitieke, *Gardner H164* (AK); Ngawaka, N of Taihape, *Druce in Oct. 1978* (CHR); Mataroa, NW of Taihape, *Druce in Feb. 1979* (CHR); Potaka Bush, Rangitkei Valley, SE of Taihape, *Druce in Nov. 1979* (CHR); Kawhatau Valley, E of Mangaweka, *Druce in Apr. 1977* (CHR); NE of Hunterville, *Druce in Dec. 1978* (CHR). **Eastern North Island:** Hangaroa Valley, W of Whakapunake, *Druce in Dec. 1967* (CHR); Waipipapoa, S of Havelock North, *Druce in Oct. 1973* (CHR); Elsthorpe Domain, Hawke Bay, *Druce in Apr. 1980* (CHR), *Elder 723/2* (CHR); Waipukurau Scenic Reserve, Hawke Bay, *Druce in Nov. 1975* (CHR); Dannevirke, *Colenso s.n.* (WELT 22767, mixed collection with *F.* ×*colensoi*); Mangapuaka Stream, E of Dannevirke, Hawkes Bay, *Druce in June 1982* (CHR). **Western North Island:** Marokopa River, W of Te Kuiti, *Druce in Oct. 1978* (CHR); Tututawa, 12 mi. E of Stratford, *Hedditch in Nov. 1966* (CHR); Gordon's Park Reserve, near Wanganui, *Raven 25132* (CHR); Okura Banks, Wanganui River, *Phillips s.n.* (AK). **Southern North Island:** E of Masterton, Wairarapa Dist., 1.5 mi. W of Carswell, *Macmillan 70/269* (CHR); Maungaraki River, Wairarapa, *Druce in Jan. 1966* (CHR); Tauweru Valley, E of Carterton, Wairarapa, *Druce in Mar. 1976* (CHR); Carter's Bush, near Ruamahanga River, *Raven 25121* (CHR, 7 sheets); Merry Hill Farm, Feilding, *Allan 173* (CHR); Kitchener Park, near Feilding, *Healy in 3 Oct. 1934* (CHR, WELT); Pohangina Valley, *Druce in Oct. 1973* (CHR); Bledisloe Park, Massey,

Raven 25123 (CHR, 3 sheets); Tiritea Stream, Fitzherbert West, *Healy s.n.* (CHR); Keeble's Bush, S of Palmerston North, *Druce in Feb. 1979* (CHR); Himatangi Bush, on Barber Estate, *Raven 25127* (CHR, 10 sheets); 0.5 mi. W of Ohau, *Duguid in 18 Oct. 1953* (CHR); Otaki Gorge, *Atkinson in 20 Feb. 1931* (WELT); Pakuratahi River, near track to Eastern Hutt, *Mason in 1 Dec. 1945* (CHR); Silverstream Bush, Hutt Valley, *Druce in Jan. 1973* (CHR); stream W of Sinclair Head, S Wellington Coast, *Ogle 434* (WELT); near Cape Terawhiti, *Healy 1023* (CHR); Red Rock Stream, 0.5 mi. from coast W of Wellington, *Raven 25206–1* (CHR). **Northern South Island:** mouth of Kohaihai River, 10 mi. N of Karamea, NW Nelson, *Macmillan 69/56* (CHR); Kahurangi Point, NW Nelson, *Collett in Mar.–Apr. 1965* (CHR); Kaihoka Point, NW Nelson, *Druce in Dec. 1978* (CHR); Motueka, *Healy in 27 Feb. 1944* (CHR); along D'Urville River near Lake Rotoroa, *Raven 25567* (CHR, 2 sheets); Canvastown, Pelorus, *Kirk in 22 Nov. 1886* (WELT); E of Taylor's Pass, S of Blenheim, Marlborough, *Druce in Nov. 1976* (CHR). **Eastern South Island:** Ngawiro, Waiau, *Simpson 8251* (CHR); hills E of Parnassus, *Robins & Mitchell in 6 Jan. 1969* (CHR); Ethelton, Hurunui River, *Healy in 20 Dec. 1943* (CHR); Lower Waipara, *Oliver in 29 Aug. 1948* (WELT); Kowai Bush, railway station between Springfield and Arthur's Pass, *Talbot in 1947* (CHR); Selwyn Gorge, *Oliver in 23 Nov. 1947* (CHR, WELT); Riccarton Bush, Christchurch, *Raven 25212* (CHR, 8 sheets); Summit Road, Kennedy's Bush, Sign of the Bellbird, *Berry & Brako 4622* (CHR); Stony Bay, N of Okain's Bay, Banks Peninsula, *Ericson in 9 Dec. 1971* (CHR); Rakaia Gorge, 8 mi. from Lake Coleridge, opp. Mt. Hutt range, *Talbot in Jan. 1949* (CHR); Mount Peel, *Allan 394* (CHR); King's Gully, Timaru, *Mason in 11 Nov. 1945* (CHR, 2 sheets); Hunters Hills, Hendry's Bush, *Macmillan & Woodhouse 72/1200* (CHR). **Western South Island:** Karamea, *Moore in 26 Dec. 1957* (CHR); 2 mi. E of Te Namu, S of Karamea, *Raven 25239* (CHR, 10 sheets); Westport Domain, SW Nelson, *Kelly & Kelly in 10 Oct. 1973* (CHR); Cape Foulwind, Westport, *Berry & Brako 4598* (CHR); Punakaiki, *Raven 25224* (CHR, 7 sheets); Paroa, S of Greymouth, *Oliver in 17 Apr. 1948* (CHR, WELT); Arnold River Scenic Reserve, Moana, *Loh in 21 Nov. 1978* (CHR); mouth of Mikonui River, *Wardle & Myers in 3 Dec. 1969* (CHR); 1 mi. N of crossing of Paringa River, S Westland, *Raven 25346* (CHR); N side of Cascade River Mouth, S Westland, *Wardle in 31 Mar. 1977* (CHR). **Southern South Island:** Pars Creek, NE of Dansey's Pass, N Otago, *Wardle in 5 Jan. 1975* (CHR); N of Hampden, E Otago, *Macmillan 72/919* (CHR); Shag River Valley, 5 mi. NW of Dunback on Highway 85, *Meurk in 24 Sep. 1971* (CHR); Otago Peninsula, Broad Bay, *Johnson in 20 Oct. 1981* (CHR); Kaitangata, E Otago, *Petrie in Oct. 1892* (WELT); Kelso, near Tapanui, Otago, *Petrie in Dec. 1886* (WELT, mixed collection with *F.* ×*colensoi*); 1.5 mi. N of Lumsden, central Otago, *Atwood in Jan. 1940* (AK); Coal Creek Rock Bluff, Umbrella Ecological District, Otago, *Dickinson & Mark in 24 Jan. 1986* (CHR, OTA); Bluff Head, S coast, *Oliver in 12-X-1945* (WELT); Oreti River, Invercargill, *Holloway s.n.* (OTA).

In the protologue to *Fuchsia perscandens*, Allan stated that his description was based on living plants growing at Kitchener Park. The lectotype here designated was annotated by Allan in September 1926 as "part of type specimens" of *F. perscandens*, and is clearly one of the plants used to

describe this species. When Allan's treatment for the Flora of New Zealand was published (Allan, 1961: 282), however, he designated an undated specimen from Kitchener Park (*Allan s.n.*, CHR 11479) as the lectotype. This choice is superseded because the specimen is a hybrid between *F. perscandens* and *F. excorticata* and is in conflict with the protologue (see also Allan, 1927, for a discussion of the hybrids at Kitchener Park). Allan did not have access to all of his original specimens when he prepared his flora, and he apparently did not consult *Allan 982a*, which then formed part of the Carse Herbarium (CANTY).

4. Fuchsia excorticata (J. R. & G. Forster) Linnaeus f., Suppl. Pl. 217. 1781. *Skinnera excorticata* J. R. & G. Forster, Char. Gen. Pl. 58, pl. 29. 1776. TYPE: New Zealand. Queen Charlotte Sound: either 2–25 Nov. 1773 or 19 Oct.–10 Nov. 1774, *G. Forster s.n.* (lectotype, selected here, Herb. Smith 670.7, LINN).

Large shrub or tree 2–13 m tall, winter deciduous in most of its range; trunk generally irregular, ± twisted, to 70 cm diam., branching within several m of the base to form a broad, spreading canopy; bark coppery light brown and papery, peeling off readily in patches or large strips, with a smooth, green cambial layer beneath the outer layers; branches subglabrous to strigulose. Leaves alternate, thick-membranous, lanceolate to ovate-elliptic, (35–)45–130 mm long, (15–)25–55 mm wide, acute to acuminate at apex, acute to rounded at base, strongly bicolored, medium to dark green above, silvery white below or occasionally suffused with red, glabrous to strigulose along the margins and veins beneath; margin entire to remotely serrulate; secondary veins 9–12 per side. Petiole 9–40 mm long, subglabrous to strigulose above. Stipules lanceolate, purplish, 1.5–4 mm long, 0.3–0.8 mm wide, drying out from the tip down, caducous. Gynodioecious. *Perfect flowers*: solitary or ± tightly grouped on shortened side shoots, sometimes appearing cauliflorous; pedicels slender, drooping in bud and flower, divergent or ascending in fruit, 5.5–15 mm long. Ovary 4.5–8 mm long, 1.7–3 mm thick, green. Floral tube 11–22 mm long, 3–5 mm wide at the bulbous base (lined by smooth nectariferous tissue inside), sharply constricted above to 1.4–2.5 mm diam., then enlarged until 4–10 mm wide at the rim, with 4 antepetalous ridges. Sepals narrow-triangular, 8–19 mm long, 3–6 mm wide at base, spreading or occasionally reflexed. Tube and sepals lustrous green at anthesis, with dull purple streaks in upper parts between the ridg-

es of the tube, both changing ± abruptly to red-crimson about halfway through anthesis. Petals dark purple, (narrowly) elliptic or lanceolate, 1.8–5 mm long, 0.7–2.1 mm wide in the middle, acute or obtuse at apex. Filaments 6–15 mm and 5–10 mm long, light to dark purple, pale cream on connective to anther; anthers 1.8–2.5 mm long, 1–1.7 mm thick, purple. Style glabrous, 22–40 mm long, purple in exserted part and greenish below; stigma capitate, 1.8–2.2 mm long, 1.4–2.1 mm wide, yellow-green. Berry oblong-ellipsoid, 9–13 mm long, 5–8 mm thick, dark purple; seeds oblong-triangular, 0.75–1 mm long, 0.3–0.6 mm broad, tan, 320–670 (mostly around 500) per fruit. *Pistillate flowers*: similar to perfect ones except: pedicels 4.5–8.5 mm long. Ovary 4–6 mm long, 2–2.5 mm wide. Floral tube 6.5–13 mm long, 4–6 mm diam. at rim. Sepals 5.5–8 mm long, 2.2–3.5 mm wide at base. Petals 1.2–2.6 mm long, 0.35–1 mm wide. Filaments 2–4 mm and 1.2–3.5 mm long; anthers aborted, 0.8–1.2 mm long, 0.6–0.9 mm wide. Style 18–23 mm long. Gametic chromosome number $n = 11$.

Common names. kotukutuku (Maori, for whole plant), konini (Maori, for the berry), tree fuchsia, native fuchsia.

Distribution. Widespread all over North Island, South Island, and Stewart Island of New Zealand, rare on Auckland and Chatham Islands, in lowland to upper montane forest, especially along margins and near streams, 0–1050 m; flowering mostly from August to December, but occasionally from as early as June or July and as late as the end of January.

Representative specimens examined. NEW ZEALAND. **Northern North Island:** Mangonui Co., Te Paki Coastal Park, 'Radar Bush', *Bartlett s.n.* (CHR 314556); Mangonui, Kaitaia, *Matthews 2311* (AK); Cavalli Islands, Motukawanui Island, ¾ way up Waiti Stream, *Court s.n.* (AK 149877); Whangarei Co., Pikiwahine-Tauraroa Rd., *Cooper s.n.* (AK 120225); Hen & Chickens Island, Hen Island, above Dragon's Mouth Cove, *Wright 2226* (AK); Little Barrier Island, *Shakespear s.n.* (AK 127539); Hobson Co., Katui, *Cooper s.n.* (AK 127370); Titirangi, near Auckland, *Carse 980/4* (CHR); Mt. Wellington lava fields, Auckland, *Petrie in Sep. 1896* (WELT); Mauku, Manukau Co., *Carse 980/8* (CHR); Hauraki Gulf, Ponui (Chamberlin's) Island, *Brown s.n.* (AK 151199); Great Barrier Island, east coast scrub-bush, N of Whangapoua Beach, *Frater, Cooper & Stephenson 355* (AK); Coromandel Co., Mercury Bay, *Wright 633* (AK); Tirau, upper Thames valley, *Petrie in Nov. 1894* (WELT); Tauranga-Hamilton old road, Kaimai Range, *Chapman in 2 Oct. 1973* (CHR); Waioeka Gorge, Opotiki Distr., *Heginbotham in Aug. 1975* (CHR); 4 mi. E of Rotoma Saddle on Rotorua-Whakatane road, *Hamilton in 3 Nov. 1970* (CHR); Lake Tarawera, *Lambrechtsen in 12 Jan. 1971* (CHR); 7 mi. N of junction near Kawhia, road to Raglan, *Raven 25181* (CHR); 6 mi. E of Waitomo, *Raven 25187* (CHR). **Central North Island:** Maraeroa, 17 mi. SE of Mangapehi, *Rawson in 20*

Jan. 1947 (CHR); Taumarunui, *Davidson in 1909* (WELT); Mt. Pihanga, Taupo, *Parsons 225* (CHR); W slopes of Mt. Tongariro, *Atkinson in 12 Jan. 1964* (CHR); Three Kings Range, Kaimanawa Range, *Druce in Jan. 1974* (CHR); 7 mi. S of Raetihi, *Raven 25134* (CHR, 2 sheets). **Eastern North Island:** Mt. Hikurangi, Raukumara Range, Gisborne Prov., *Veitch s.n.* (CHR 191554); Pakihiroa, *Oliver in 16 Nov. 1926* (WELT); Huiarau Range, highest point, *Lambrechtsen in 11 Jan. 1971* (CHR); N of Te Haroto, Hawke Bay, *Macmillan 72/1021* (CHR); Maraetotara Valley, S of Havelock North, *Druce in Oct. 1973* (CHR). **Western North Island:** 0.5 mi. below Marokopa Falls, near Te Anga, *Lambrechtsen in 14 Jan. 1971* (CHR); Dawson Falls, Mt. Egmont, *Heine in 29 Dec. 1932* (WELT); Opunake, *Druce in Nov. 1970* (CHR); Tokomaru E Road, Wanganui, *Wanganui Museum Botanical Group 40* (CHR). **Southern North Island:** Ruahine-Cook, Rangitikei Gorge, *Zotov 193* (CHR); Alfredton, Wairarapa District, E of Eketahuna, *Macmillan 70/277* (CHR); Heatherlea East, N of Levin, *Duguid s.n.* (CHR 194271); Bannister's Hut, Mt. Holdsworth, *Heine in 14 Jan. 1930* (WELT); Kahoa Stream, Pukerua Bay, *Ogle in 12 Sep. 1974* (WELT); Park Vale, Karori, *Kirk in 8 Nov. 1883* (WELT, 3 sheets); Palliser, *Healy s.n.* (WELT); Haurangi Mts., *Oliver in 7 Dec. 1930* (WELT, 3 sheets). **Northern South Island:** bluff behind cottage SW of Kaihoka Lakes, *Given 69879* (CHR); Karamea, in carpark at Oparara Arches, *Manning in 15 Dec. 1984* (CHR); Riwaka River, N.W. Nelson, 300 ft., *Druce in Nov. 1974* (CHR); 5.5 mi. W of Murchison, *Godley in 3 Feb. 1971* (CHR); Capleston Reserve, N of Reefton, *Macmillan in 25 Jan. 1972* (CHR); near Maruia Springs, 800 m, *Berry & Brako 4596* (CHR); Tennyson Inlet, Marlborough Sounds, *Hynes in 16 Feb. 1969* (CHR); Canvastown, Pelorus, *Kirk in 22 Nov. 1886* (WELT); Shin Creek, inland Kaikoura, *Hamlin 919* (WELT); Lynton Downs, Kaikoura, *Kirk in Dec. 1889* (WELT). **Eastern South Island:** Lewis Pass Rd., near junction of Doubtful and Boyle Rivers, *Godley in 3 Feb. 1971* (CHR); upper Hurunui River, 2 mi. W of Lake Sumner, *Macmillan & Stemmer in 29 Jan. 1973* (CHR); Motunau River, N Canterbury, *Mason & Simpson in 22 Nov. 1960* (CHR); View Hill Reserve, Oxford, *Moore in 11 Oct. 1969* (CHR); Woodstock, *Moore in 3 Jan. 1971* (CHR); Riccarton Bush, Christchurch, *Raven et al. 25214* (CHR); near Cass Peak, Port Hills, *Macmillan in July 1964* (CHR); head of Kaituna Valley, Banks Peninsula, *Kelly in 18 Nov. 1965* (CHR); NW of Staveley, Ashburton County, *Macmillan in 30 Sep. 1970* (CHR); Peel Forest, South Canterbury, *Rawson in 2 Oct. 1974* (CHR); Bluecliffs Station, Hunters Hills, South Canterbury, *Sykes in 14 Apr. 1971* (CHR). **Western South Island:** Punakaiki, *Raven 25222* (CHR); 1 mi. S of Barrytown, *Raven 25219* (CHR); Crushington, near Reefton, *Molloy in 4 Mar. 1988* (CHR); Omotomotu Scenic Reserve, *Loh in 16 Nov. 1978* (CHR); Otira Gorge, *Raven 25334* (CHR); E of Kumara, *Berry & Brako 4615* (CHR); near Hokitika, *Woods in 29 Nov. 1987* (CHR); foot of Mt. Hercules, *Wardle in 30 Nov. 1970* (CHR); Lake Wahapo, *Wardle in 30 Nov. 1970* (CHR); valley just below Franz Josef Glacier, *Raven 25337* (CHR); Bruce Bay, south Westland, *Wardle in 7 Jan. 1977* (CHR); Haast River, at Thundering Falls, *Raven 25358* (CHR). **Southern South Island:** Leith Valley, Dunedin, *Oliver in Dec. 1940* (WELT); Hoopers Inlet, Otago Peninsula, *Johnson in 17 Oct. 1971* (OTA); Tautuku Reserve, South Otago, *Esler in Jan. 1978* (OTA); Dunsdale, Hokonui Hills, Southland, *Miller in 17 Apr. 1976* (OTA); Luggate Creek, Pisa Range, 1100 ft., *Mark & Wells*

in 1 Dec. 1966 (OTA); Lake Wakatipu shore, *Oliver in 11 Feb. 1953* (WELT); Falls Creek, upper Hollyford valley, *Salmon in Dec. 1943* (WELT); Milford side of Homer Tunnel, Fiordland, *Enting in 13 Apr. 1973* (WELT); Divide Creek, N of Lake Fergus, *Raven 25431* (CHR); head of Stillwater River, Fiordland, *Anderson in 2 Jan. 1971* (CHR); Lake Shirley, Fiordland, *Given 69543* (CHR); Lake Manapouri, head of South Arm, *Raven 25420* (CHR); Deep Cove, Doubtful Sound, *Macmillan in 12 Dec. 1962* (CHR); Hut Creek, Supper Cove, Dusky Sound, Fiordland, *Given 72545* (CHR); Wet Jacket Arm, valley S of Mt. Anderson, Fiordland, *Given 72207* (CHR). **Stewart Island:** N Arm, Port Pegasus, *Ritchie in 22 Feb. 1966* (CHR); Deep Bay, Paterson Inlet, *Wilson 789–85* (CHR); Half-Moon Bay, *Brownlie 84* (CHR); Ernest Island off Port Pegasus, *Yaldwyn in 1 Mar. 1972* (WELT); road to Fern Gully, *Goulding 761* (AK), *762* (AK). **Chatham Island:** S of Lake Huro, *Hamel in 28 Jan. 1976* (CHR, OTA); Te Awatea, S shore of Lake Huro, *Given & Williams 13023* (CHR); by Lake Huro, *Ritchie & Ritchie in 16 Sep. 1968* (CHR); Maipito Bush, Waitangi, *Hamel in 29 Jan. 1976* (OTA). **Auckland Island:** Auckland Is., *Aston in Jan. 1909* (AK, WELT); Port Ross, *Aston s.n.* (WELT); Laurie Harbour, *Dawbin in 25 Aug. 1943* (CHR), *Oliver in 27 Mar. 1927* (WELT); mouth of Grey Duck Stream, *Godley in 29 Dec. 1962* (CHR).

5. Fuchsia ×colensoi Hooker f. (pro sp.), Handbk. N. Z. Fl. 728. 1867. TYPE: New Zealand. North Island: from woods at Titiokura, *William Colenso 1048* (lectotype, selected here, K; Fig. 38).

Fuchsia ×experscandens Allan, Genetica 9: 507, fig. 5. 1927. TYPE: New Zealand. North Island: forest remnants near Feilding, Merry Hill Farm, Feilding, *H. H. Allan in Sep. 1926* (lectotype, selected here, CHR 11523). There are six sheets numbered 11519–11524 at CHR, and the lectotype is from a female plant.

Small to large shrubs or small trees, the main branches upright, scandent-climbing or decumbent; main stem to 30 cm diam.; bark papery, copper-colored, readily flaking off; branchlets subglabrous to strigulose. Leaves alternate, thick-membranous, usually broadly elliptic-ovate, lance-ovate or suborbicular, 18–85 mm long, 10–45 mm wide, obtuse to acute at apex, truncate to obtuse or subcordate at base, pale green above, paler green to whitish beneath, glabrous to strigulose along the margins and veins beneath; margin entire to serrulate with small, glandular teeth; secondary veins (5)6–8(9) per side. Petiole slender, 5–50 mm long, subglabrous to strigulose above, sometimes with a semipersistent swollen base. Stipules triangular, 0.8–2.4 mm long, 0.4–1.1 mm wide, semisucculent and purple when young, quickly drying from the tip, caducous.

Gynodioecious, the flowers intermediate in size between *F. excorticata* and *F. perscandens*. *Perfect flowers:* pedicels slender, hanging, 5–14 mm long.
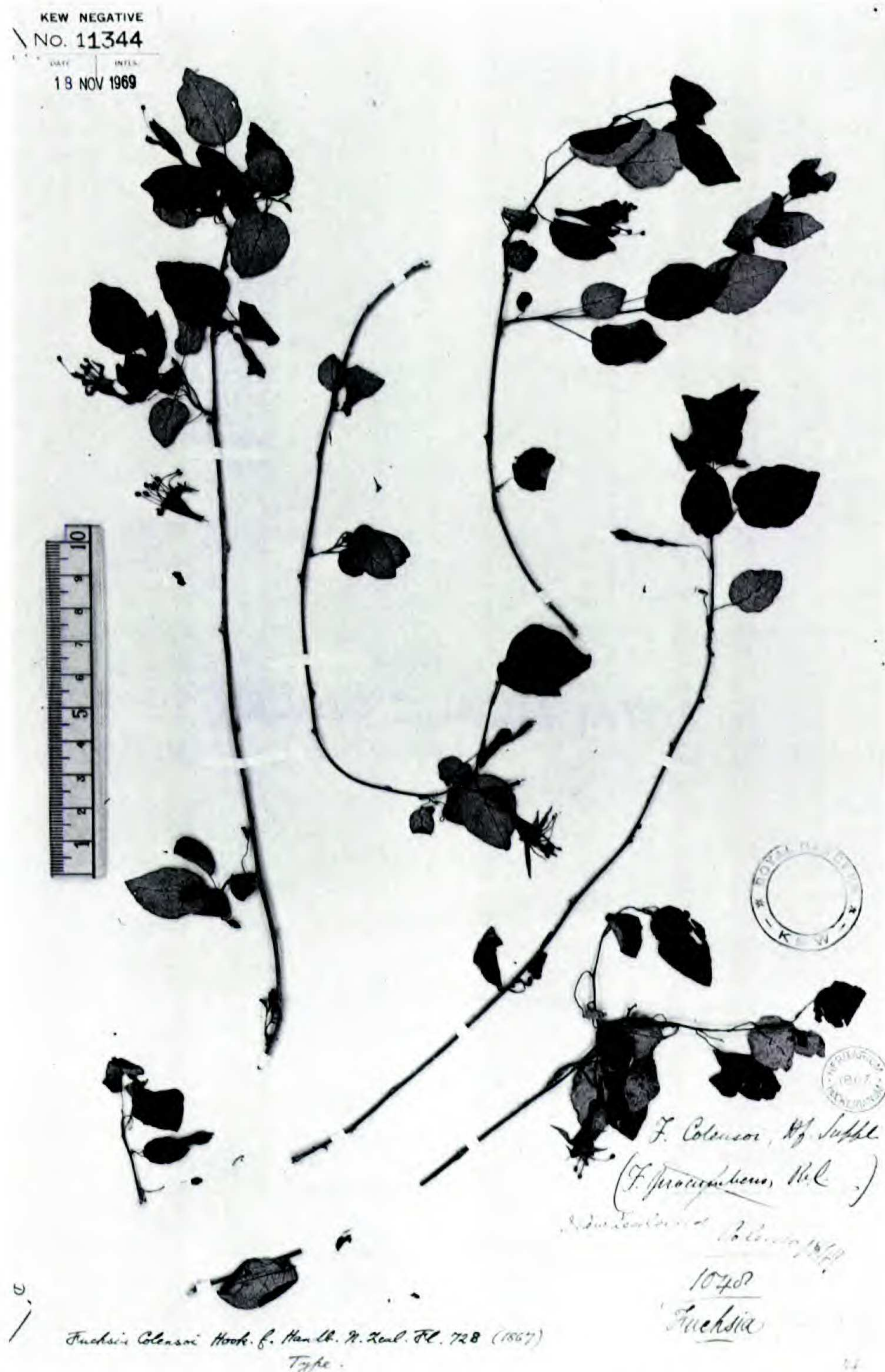
FIGURE 38. Lectotype of *F.* ×*colensoi*. Photograph courtesy of the Royal Botanic Gardens, Kew.

Ovary 4–7 mm long, 1.6–2.5 mm thick, green. Floral tube 9–20 mm long, 2.5–4.2 mm wide and bulbous at the base, constricted above to 1.2–2.3 mm wide, then ampliate until 4–9 mm wide at the rim. Sepals narrow-triangular, 7–14 mm long, 3.5–5 mm wide at base, spreading. Tube and sepals lustrous green at anthesis with dull purple streaks in the upper tube, changing to dull red or bright crimson before deshiscing. Petals dark purple, elliptic, 1–5 mm long, 0.7–1.5 mm wide in the middle. Filaments 7–15 mm and 5–8 mm long, purple, with pale cream connective; anthers 1.7–2.6 mm long, 1–1.8 mm wide, purple. Style 20–37 mm long,

cream to light purple; stigma 1.5–2.1 mm long, 1.1–2 mm wide, yellow-green. Berry oblong to subglobose, 9–11 mm long, 5–7 mm thick, red-purple; seeds oblong-triangular, 0.8–1.1 mm long, 0.4–0.6 mm wide, 240–500 per fruit. *Pistillate flowers*: similar to perfect ones except: floral tube 6–12 mm long, 3.5–5.5 mm wide at rim. Sepals 5–10 mm long, 2.5–3.5 mm wide at base. Petals 1.1–2.4 mm long, 0.3–1.1 mm wide. Filaments 2.5–6 mm and 1.6–5 mm long; anthers aborted, 0.7–1.1 mm long, 0.5–0.8 mm wide. Style 16–30 mm long. Gametic chromosome number $n = 11$ (no meiotic irregularities observed).

Distribution. Widespread from 38°16'S south through the North and South Islands of New Zealand, also Stewart Island, sea level to 300 m; flowering mostly from August to January, occasionally earlier in some localities.

Representative specimens examined. NEW ZEALAND. **Northern North Island:** entrance to Aranui Cave, Waitomo Caverns, *Raven 25193* (CHR, 3 sheets); Mangapu Stream, 5 km NW of Te Kuiti, Waitomo Co., *Gardner 3143* (AK). **Central North Island:** Taumarunui W, Wanganui River Flat, *Atwood in Nov. 1937* (CHR); Ohinewairua, Kaimanawa Mts., *Druce in Apr. 1976* (CHR); Moawhango River, NE of Taihape, *Druce in Oct. 1982* (CHR); Peak Hill, NW Ruahine Range, *Druce in Jan. 1973* (CHR). **Eastern North Island:** Ball's Clearing, Puketitiri, *Druce in Mar. 1972* (CHR); Waipoapoa, S of Havelock North, *Druce in Oct. 1973* (CHR); Maungaharuru Range, SE of Kopua, *Druce in Dec. 1972* (CHR); Dannervirke, *Colenso s.n.* (WELT, 2 sheets). **Southern North Island:** Puketoi Range, S Hawke Bay, *Druce in Dec. 1973* (CHR); Ruakokoputama Valley, Aorangi Range, *Druce in Dec. 1970* (CHR); 2.5 mi. N of Pohangina, *Raven 25129* (CHR, 10 sheets); Merry Hill Farm, Feilding, *Allan in Sep. 1926* (CHR, 6 sheets); Bledisloe Park, Massey, *Raven in 14 Oct. 1969* (CHR); Ohau River, Tararua Range, *Oliver in 6 Apr. 1941* (WELT); Lake Papaitonga, *Mason in 3 Mar. 1942* (CHR, 2 sheets); near Lake Waitawa, N of Otaki, *Duguid in 13 Dec. 1970* (CHR); Silverstream Bush, Hutt Valley, *Druce in Mar. 1976* (CHR); Island Bay, Wellington, *Phillips s.n.* (AK). **Northern South Island:** Kaihoka coast, NW Nelson, *Druce in Nov. 1974* (CHR); 2 mi. E of Te Namu, S of Karamea, *Raven 25238* (CHR); Mokihinui River, *Robins in Dec. 1970* (CHR); Therus Creek Basin, Cobb Valley, NW Nelson, *Druce in Jan. 1979* (CHR); Maitai Valley, Nelson, *Mellor s.n.* (WELT); along D'Urville River near Lake Rotoroa, *Raven 25566* (CHR); Springs Junction, 4 mi. S of Shenandoah, Nelson, *Godley in 3 Feb. 1971* (CHR); Canvastown, Pelorus, *Kirk in 22 Nov. 1886* (WELT); Waiau Valley, *Oliver in 20 Dec. 1947* (CHR, WELT); Haldon Hills, Marlborough, *Given in 31 Dec. 1978* (CHR); Lynton Downs, Kaikoura, *Kirk in Dec. 1889* (WELT). **Eastern South Island:** Gore Bay, N of Hurunui River, *Mason 7861* (CHR); Mt. Cass, SE of Waipara, *Macmillan in 14 Oct. 1962* (CHR); Riccarton Bush, Christchurch, *Raven 35313* (CHR, 36 sheets); Jollie's Bush, Summit Road above Sumner, Banks Peninsula, *Berry & Brako 4624* (CHR); Summit Road above Takamatua Bay, Akaroa Harbour, Banks Peninsula, *Macmillan 68/48* (CHR); Scott's Stream, Mt. Hutt Range, *Cartman in 5 Feb. 1978* (CHR); Alford Forest, S Canterbury, *Simpson 6123* (CHR), *6124* (CHR); Bowyer's Stream, end of Staveley-Sharplin Falls Rd., Alford Forest, *Drury ASH15* (CHR); Winterslow, Taylor's Stream, *Canterbury Bot. Soc. in 8 Jan. 1973* (CHR); Peel Forest, S Canterbury, *Godley in 2 Oct. 1954* (CHR, 3 sheets); ca. 10 mi. E of Geraldine on road to Fairlie, *Raven 25272* (CHR); Hunter's Hills, Blue Cliffs Station, S Canterbury, *Macmillan 72/1355* (CHR), *73/711* (CHR). **Western South Island:** Cape Foulwind, W of Westport, *Berry & Brako 4599* (CHR); 5 mi. N of Punakaiki, *Raven 25227* (CHR); 1 mi. S of Barrytown, *Raven 25220* (CHR, 4 sheets); Lake Ryan Scenic Reserve, Greymouth, *Loh in 13 Nov. 1978* (CHR); Mananui, *Attwood s.n.* (CHR); mouth of Mikonui River, near Ross, *Wardle & Myers in 3 Dec. 1969* (CHR); head of Okarito Lagoon, *Mason & Moar in 24 Feb. 1958* (CHR); S of Lake Mapourika, *Mason & Moar in 17 Feb. 1958* (CHR); N side of Potter's Creek, *Berry & Brako 4606* (CHR); track to Callery Springs, Franz Josef, *Wardle in 2 Dec. 1970* (CHR); 1 mi. N of Paringa River crossing, *Raven 25347* (CHR); 4.2 mi. E of turn to Haast Township, *Raven 25353* (CHR). **Southern South Island:** Port Chalmers, *Cockayne 4109* (WELT); near Dunedin, *Petrie in 1890* (WELT); Otago Peninsula, High Road, ca. 2 mi. E of Centre Road, *Raven 25112* (CHR); Portobello Peninsula, Otago Peninsula, *Johnson in 15 Feb. 1982* (CHR); Waipori Gorge, Otago, *Mason 837* (CHR); Tautuku Bay, Catlins, *Wardle in Nov. 1964* (CHR); Kelso, near Tapanui, Otago, *Petrie in Dec. 1888* (WELT); Spar Bush, Southland, *Powell s.n.* (CHR); Lind's Crossing, Southland, *Kirk in 10 Dec. 1883* (WELT, 3 sheets); Sandy Point, Invercargill, *Raven 25097* (CHR); Bluff, *in Nov. 1907* (WELT 24850). **Stewart Island:** The Neck, near Angela Point, *Wilson 789-559* (CHR).

The lectotype locality of *Fuchsia* ×*colensoi*, Titiokura Saddle, is located in the Moungaharuru Range, ca. 53 km from Napier. Allan (1961: 283) cited *Colenso 144* at K as the type for *F. colensoi*, but his choice is superseded because Hooker only questionably accepted this specimen as belonging to the taxon. Of the five possible syntypes at K, the only one without a clear determination in Hooker's hand is *Colenso 144*, which he annotated in pencil as "*F. Colensoi* ? small var." The other four, including *Colenso 1048*, are annotated by him in ink as *F. colensoi*, without any query.

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Appendix.   Index of collections examined.

1. *Fuchsia procumbens* R. Cunningham ex A. Cunningham
2. *Fuchsia cyrtandroides* J. W. Moore
3. *Fuchsia perscandens* Cockayne & Allan
4. *Fuchsia excorticata* (J. R. & G. Forster) Linnaeus f.
5. *Fuchsia* ×*colensoi* Hooker f.

Adams s.n. (AK 15112, 15113) **4**, s.n. (AK) **1**, s.n. (WELT) **1**; Alford in 26 Apr. 1934 (WELT) **4**; Allan 173 (CHR) **3**, 394 (CHR) **3**, 982a (CHR) **3**, in Sep. 1926 (CHR 11519–11524) **5**, s.n. (CHR 11526) **4**, s.n. (WELT 8379, mixed collection with 4 and 5) **3**, 29365 (CHR) **1**; Anderson in 2 Jan. 1971 (CHR) **4**; Aston in Jan. 1909 (AK, WELT) **4**, s.n. (AK 5899) **4**, s.n. (WELT) **4**; Atkinson in 20 Feb. 1931 (WELT) **3**, in 12 Jan. 1964 (CHR) **4**; Atwood in Nov. 1937 (CHR) **5**, in Jan. 1940 (AK) **3**, s.n. (AK) **5**.

Banks & Solander s.n. (AK 101152) **4**; Bartlett N40 (CHR) **1**, TV181 (CHR) **3**, s.n. (CHR 314556) **4**; Bellingham s.n. (AK 168940) **4**; Berry & Brako 4596 (CHR) **4**, 4598 (CHR) **3**, 4599 (CHR) **5**, 4600 (CHR) **5**, 4601 (CHR) **5**, 4602 (CHR) **4**, 4603 (CHR) **5**, 4605 (CHR) **5**, 4606 (CHR) **5**, 4608 (CHR) **5**, 4609 (CHR) **3**, 4611 (CHR) **3**, 4612 (CHR) **5**, 4613 (CHR) **5**, 4614 (CHR), 4615 (CHR) **4**, 4622 (CHR) **3**, 4624 (CHR) **5**, 4626 (AK, MO) **1**, 4627 (AK, MO) **1**; Berry et al. 4587 (CHR) **3**, 4588 (CHR) **5**, 4589 (CHR) **5**, 4590 (CHR) **5**, 4591 (CHR) **5**, 4628 (PAP, MO) **2**; Bluff in Nov. 1907 (WELT 24850) **5**; Bowman in 26 Dec. 1975 (CHR) **4**, s.n. (AK

151199) **4**; Brownlie 84 (CHR) **4**; Burke, G.K.R. & W.D., s.n. (WELTU) **1**; Burrell s.n. (CHR 133367) **4**.

Canterbury Bot. Soc. in 13 Mar. 1971 (CHR) **5**, in 8 Jan. 1973 (CHR) **5**; Carlquist 653 (DS—2 sheets, RSA) **2**; Carse 980/4 (CHR) **4**, 980/8 (CHR) **4**, 980/11 (CHR) **4**, 982 (CHR) **1**, 982/A (CHR) **1**, s.n. (CHR) **1**, s.n. (WELT) **1**; Cartman in 5 Feb. 1978 (CHR) **5**; Chapman in 2 Oct. 1973 (CHR) **4**, s.n. (CHR 239330) **4**; Cheeseman in Jan. 1875 (AK, 2 sheets) **3**, in Jan. 1884 (AK) **3**, s.n. (AK 101154) **1**, s.n. (AK 101155) **1**, s.n. (AK 5895) **4**, s.n. (AK) **1**, s.n. (AK, 2 sheets; WELT) **1**; Cockayne 4109 (WELT) **5**; Colenso 1048 (K) **5**, s.n. (WELT 22767, mixed collection with 5) **3**, s.n. (WELT, 2 sheets) **5**; Collett in Mar.–Apr. 1965 (CHR) **3**; Collis in 14 Nov. 1964 (AK) **3**; Cooper s.n. (AK 117989) **4**, s.n. (AK 117990) **4**, s.n. (AK 118459) **4**, s.n. (AK 118991) **4**, s.n. (AK 119899) **4**, s.n. (AK 120089) **4**, s.n. (AK 120225) **4**, s.n. (AK 125670) **4**, s.n. (AK 125671) **4**, s.n. (AK 125711) **4**, s.n. (AK 125760) **4**, s.n. (AK 126195) **4**, s.n. (AK 126196) **4**, s.n. (AK 126354) **4**, s.n. (AK 126467) **4**, s.n. (AK 126801) **4**, s.n. (AK 127333) **4**, s.n. (AK 127370) **4**, s.n. (AK 127371) **4**, s.n. (AK 128220 and AK 128223) **4**, s.n. (CHR 194295) **4**, s.n. (CHR 194296) **4**; Court s.n. (AK 149877) **4**; Cragg in 22–28 Mar. 1973 (CHR) **4**; Cunningham, R. (K) **1**.

Davey s.n. (CHR 194272) **4**; Davidson in 1909 (WELT) **4**; Davidson & Petrie in Nov. 1908 (WELT) **3**; Dawbin in 25 Aug. 1943 (CHR) **4**; de Lange in 21 Oct. 1984 (AK) **3**, in 6 Feb. 1985 (AK) **3**, in 4 Dec. 1991 (AK) **3**; Dickson s.n. (AK 140298) **4**, s.n. (AK, CHR) **1**; Dickinson & Mark in 24 Jan. 1986 (CHR, OTA) **3**; Druce in Jan. 1966 (CHR) **3**, in Feb. 1967 (CHR) **3**, in Dec. 1967 (CHR) **3**, in Feb. 1970 (CHR) **4**, in Nov. 1970 (CHR) **4**, in Dec. 1970 (CHR) **5**, in Mar. 1971 (CHR) **3**, in June 1971 (CHR) **3**, in Feb. 1972 (CHR) **5**, in Mar. 1972 (CHR) **5**, in Oct. 1972 (CHR) **3**, in Nov. 1972 (CHR) **3**, in Nov. 1972 (CHR) **5**, in Dec. 1972 (CHR) **5**, in Jan. 1973 (CHR) **3**, in Jan. 1973 (CHR) **5**, in Apr. 1973 (CHR) **4**, in June 1973 (CHR) **3**, in Oct. 1973 (CHR) **3**, in Oct. 1973 (CHR) **4**, in Oct. 1973 (CHR) **5**, in Dec. 1973 (CHR) **5**, in Jan. 1974 (CHR) **4**, in Nov. 1974 (CHR) **3**, in Nov. 1974 (CHR) **4**, in Nov. 1974 (CHR) **5**, in Nov. 1975 (CHR) **3**, in Feb. 1976 (CHR) **3**, in Mar. 1976 (CHR) **3**, in Mar. 1976 (CHR) **5**, in Apr. 1976 (CHR) **5**, in Oct. 1976 (CHR) **3**, in Nov. 1976 (CHR) **3**, in Jan. 1977 (CHR) **4**, in Apr. 1977 (CHR) **3**, in Oct. 1978 (CHR) **3**, in Dec. 1978 (CHR) **3**, in Jan. 1979 (CHR) **5**, in Feb. 1979 (CHR) **3**, in Nov. 1979 (CHR) **3**, in Apr. 1980 (CHR) **3**, in June 1982 (CHR) **3**, in Oct. 1982 (CHR) **3**, in Oct. 1982 (CHR) **5**, s.n. (CHR 129787) **4**, s.n. (CHR 129788) **4**, s.n. (CHR 158729) **4**, s.n. (CHR 180891) **4**, s.n. (CHR 208680) **4**, s.n. (CHR 210044) **4**, s.n. (CHR 210450) **4**, s.n. (CHR 244274) **4**, s.n. (CHR 244927) **4**, s.n. (CHR 262318) **4**, s.n. (CHR 282807) **4**, s.n. (CHR 86602) **4**, s.n. (CHR) **3**; Drury ASH15 (CHR) **5**; Duguid in 18 Oct. 1953 (CHR) **3**, in 13 Dec. 1953 (CHR) **3**, in 13 Dec. 1970 (CHR) **5**, s.n. (CHR 194263) **4**, s.n. (CHR 194268) **4**, s.n. (CHR 194269) **4**, s.n. (CHR 194270) **4**, s.n. (CHR 194271) **4**, s.n. (CHR 194274) **4**, s.n. (CHR 194275) **4**.

Elder 723/2 (CHR) **3**; Engelhorn 15282 (CHR) **5**, 25284 (CHR) **3**, 25714 (CHR) **1**, 25719 (CHR, 3 sheets), 25720 (CHR) **1**, in 25 Nov. 1969 (CHR) **4**; Enting in 13 Apr. 1973 (WELT) **4**; Ericson in 12 Dec. 1970 (CHR) **3**, in 9 Dec. 1971 (CHR) **3**; Esler 3629 (CHR) **1**; Esler 3630 (CHR) **1**, in Jan. 1978 (OTA) **4**; Evetts (AK 135484) **4**.

Florence 4700 (BISH, K, NY, P, PAP, US) **2**, 5455

(BISH, P, PAP, US) **2**, 7631 (BISH, K, P, PAP) **2**, 7748 (PAP) **2**; Florence & Guérin 2713 (PAP—2 sheets) **2**; Flynn & Flynn 329 (PAP) **2**; Forester s.n. (AK 168954) **4**; Forster s.n. (LINN, Herb. Smith 670.7) **4**; Fosberg 61095 (CHR) **2**, 62646 (CHR) **2**; Frater et al. 355 (AK) **4**, s.n. (AK) **4**.

Gardner 3142 (AK, WELT) **3**, 3143 (AK) **5**, H164 (AK) **3**; Given 69543 (CHR) **4**, 69879 (CHR) **4**, 70232 (CHR) **4**, 70590 (CHR) **4**, 70598 (CHR) **4**, 70685 (CHR) **4**, 70696 (CHR) **4**, 70771 (CHR) **4**, 72207 (CHR) **4**, 72381 (CHR) **4**, 72545 (CHR) **4**, 72600 (CHR) **4**, 72652 (CHR) **4**, in 31 Dec. 1978 (CHR) **5**; Given & Bell 70652 (CHR) **4**; Given & Williams 13023 (CHR) **4**; Godley G1785 (CHR, 2 sheets) **1**, G1786 (CHR, 2 sheets) **1**, G1787 (CHR, 2 sheets) **1**, G2201 (CHR) **1**, G2202 (CHR, 2 sheets) **1**, G2203 (CHR, 2 sheets) **1**, G2206 (CHR, 2 sheets) **1**, G2207 (CHR) **1**, G2208 (CHR, 2 sheets) **1**, G2209 (CHR, 2 sheets) **1**, G2210 (CHR) **1**, G2211 (CHR) **1**, in 2 Oct. 1954 (CHR, 3 sheets) **5**, in 29 Dec. 1962 (CHR) **4**, in 3 Feb. 1971 (CHR) **4**, in 3 Feb. 1971 (CHR) **5**, s.n. (CHR 117496) **1**; Godley & Smith 56 (CHR) **3**; Goulding 761 (AK) **4**, 762 (AK) **4**; Grace & Scott s.n. (AK 162897) **4**; Grant 3742 (A, BISH, K) **2**.

Hag s.n. (CHR 73525) **4**; Hamel in 3 Nov. 1970 (CHR) **4**, in 28 Jan. 1976 (CHR, OTA) **4**, in 29 Jan. 1976 (OTA) **4**; Hamilton s.n. (CHR 194294) **4**, s.n. (CHR) **4**; Hamlin 919 (WELT) **4**, s.n. (CHR 81823) **4**; Healy 1023 (CHR) **3**, 173 (CHR) **3**, 443 (CHR) **3**, 444 (CHR) **3**, in 31 Dec. 1932 (WELT) **4**, in 3 Oct. 1934 (CHR, WELT) **3**, in 1 Nov. 1940 (CHR) **3**, in 20 Dec. 1943 (CHR) **3**, in 27 Feb. 1944 (CHR) **3**, s.n. (CHR) **3**, s.n. (WELT) **3**, s.n. (WELT) **4**; Hector in Dec. 1862 (K) **5**; Hedditch in Nov. 1966 (CHR) **3**; Heginbotham in Aug. 1975 (CHR) **4**; Heine 14 Jan. 1930 (WELT) **4**, in 13 Nov. 1931 (WELT, 2 sheets) **4**, in 29 Dec. 1932 (WELT) **4**; Holloway in 19 Nov. 1980 (CHR) **3**, s.n. (OTA) **3**; Hutson s.n. (CHR 67808) **4**; Hynes in 23 Dec. 1966 (AK) **3**, in 28 Jan. 1967 (AK) **5**, in 16 Feb. 1969 (CHR) **4**, s.n. (AK 104136) **4**, s.n. (AK 110353) **4**, s.n. (AK 117275) **4**, s.n. (AK 120408) **4**, s.n. (AK 129117) **4**, s.n. (AK 144190) **4**; Hynes & Lynch s.n. (AK 126715) **4**.

Johnson in 17 Oct. 1971 (OTA) **4**, in 20 Oct. 1981 (CHR) **3**, in 15 Feb. 1982 (CHR) **5**, s.n. (CHR 261595) **4**.

Kelly in 23 Sep. 1965 (CHR) **3**, in 28 Oct. 1965 (CHR) **3**, in 18 Nov. 1965 (CHR) **4**; Kelly & Kelly in 10 Oct. 1973 (CHR) **3**; Kennedy s.n. (WELT) **4**; Kirk 62 (K) **1**, 79 (WELT) **1**, 192 (AK, CHR) **4**, 194 (CHR) **1**, in 10 Dec. 1883 (WELT, 3 sheets) **5**, in 8 Nov. 1883 (WELT, 3 sheets) **4**, in 22 Nov. 1886 (WELT) **3**, in 22 Nov. 1886 (WELT) **4**, in 22 Nov. 1886 (WELT) **5**, in Dec. 1889 (WELT) **4**, in Dec. 1889 (WELT) **5**, s.n. (AK 11473) **1**, s.n. (AK 15117) **1**, s.n. (AK 5909) **1**, s.n. (CHR) **1**, s.n. (WELT 24809 and 24837) **1**, s.n. (WELT 24823) **1**, s.n. (WELT) **1**, s.n. (WELT) **3**.

Lambrechtsen in 11 Jan. 1971 (CHR) **4**, in 12 Jan. 1971 (CHR) **4**, in 14 Jan. 1971 (CHR) **4**, s.n. (CHR 367024) **4**, s.n. (CHR 367025) **4**, s.n. (CHR 367026) **4**, s.n. (CHR 367027) **4**; Langbern 1/2 (CHR) **3**; Leahy s.n. (AK 137014) **4**; Lindsay in 6 Nov. 1861 (K) **5**; Lloyd s.n. (CHR) **1**; Lloyd, R. 71615 (CHR) **1**; Loh in 13 Nov. 1978 (CHR) **5**, in 16 Nov. 1978 (CHR) **4**, in 21 Nov. 1978 (CHR) **3**; Lush in 25 Mar. 1951 (CHR) **3**.

MacDaniels 1315 (BH, BISH) **2**, 1341 (BISH) **2**; Maclet 156 (CHR) **2**; Macmillan 68/35 (CHR) **3**, 68/47 (CHR) **3**, 68/48 (CHR) **5**, 69/56 (CHR) **3**, 70/269 (CHR) **3**, 70/277 (CHR) **4**, 70/288 (CHR 215233) **4**, 72/1021 (CHR) **4**, 72/1226 (CHR) **3**, 72/1355 (CHR) **5**, 72/919

(CHR) **3**, 73/711 (CHR) **5**, 79/193 (CHR) **3**, in 14 Oct. 1962 (CHR) **5**, in 12 Dec. 1962 (CHR) **4**, in July 1964 (CHR) **4**, in 30 Sep. 1970 (CHR) **4**, in 25 Jan. 1972 (CHR) **4**; Macmillan & Stemmer in 29 Jan. 1973 (CHR) **4**; Macmillan & Woodhouse 72/1200 (CHR) **3**; Manning in 15 Dec. 1984 (CHR) **4**; Mark & Wells in 1 Dec. 1966 (OTA) **4**; Mason 11831 (CHR) **4**, 11860 (CHR) **4**, 12986 (CHR) **5**, 7861 (CHR) **5**, 837 (CHR) **5**, 8876A (CHR 121153) **4**, in 10 Jan.1944 (CHR) **5**, in 11 Nov. 1945 (CHR, 2 sheets) **3**, in 3 Mar. 1942 (CHR, 2 sheets) **5**, in 31 Mar. 1945 (CHR) **5**, in 1 Dec. 1945 (CHR) **3**, in 1 Dec. 1945 (CHR) **5**; Mason & Moar 1713 (CHR) **3**, 1714 (CHR) **3**, 5714 (CHR) **3**, in 17 Feb. 1958 (CHR) **5**, in 24 Feb. 1958 (CHR) **5**; Mason & Simpson in 22 Nov. 1960 (CHR) **4**; Matthews 15 (AK) **4**, 2310 (AK) **4**, 2311 (AK) **4**, s.n. (AK 5898) **4**, s.n. (AK) **1**; Matthews, H.B. & Carse 982/2 (CHR) **1**, 982/4 (CHR) **1**; Matthews, R.H., 982/1 (CHR) **1**, 982/3 (CHR) **1**, s.n. (AK) **1**; Mellor s.n. (WELT) **5**; Meurk in 24 Sep. 1971 (CHR) **3**; Miller in 17 Apr. 1976 (OTA) **4**; Molloy in 17 Nov. 1976 (CHR) **5**, in 4 Mar. 1988 (CHR) **4**; Moore 22139 (CHR) **1**, in 11 Oct. 1969 (CHR) **4**, in 12 Oct. 1953 (CHR, 2 sheets) **3**, in 26 Dec. 1957 (CHR) **3**, in 3 Jan. 1971 (CHR) **4**.

Ogle 57 (CHR) **3**, 96 (CHR) **1**, 386 (CHR) **1**, 387 (CHR) **1**, 430 (WELT) **3**, 434 (WELT) **3**, 563 (CHR) **3**, 726 (CHR) **3**, 1381 (CHR) **3**, in 12 Sep. 1974 (WELT) **4**; Oliver in 16 Nov. 1926 (WELT) **4**, in 27 Mar. 1927 (WELT) **4**, in 10 Oct. 1930 (WELT) **3**, in 7 Dec. 1930 (WELT, 3 sheets) **4**, in Dec. 1940 (WELT) **4**, in 6 Apr. 1941 (WELT) **5**, in 12 Oct 1945 (WELT) **3**, in 13 Dec. 1947 (CHR, WELT) **3**, in 20 Dec. 1947 (CHR, WELT) **5**, in 23 Nov. 1947 (CHR, WELT) **3**, in 10 Apr. 1948 (CHR, WELT) **3**, in 10 Apr. 1948 (CHR) **5**, in 16 Apr. 1948 (WELT) **3**, in 17 Apr. 1948 (CHR, WELT) **3**, in 29 Aug. 1948 (WELT) **3**, in 6 Sep 1948 (WELT) **3**, in 1 Oct. 1949 (WELT) **3**, in 11 Feb. 1953 (WELT) **4**; Olsen 2 (AK) **1**, N16/90–31 (AK) **1**; Olsen s.n. (AK) **1**, s.n. (Godley G2204, CHR, 2 sheets) **1**; Orchard 3553 (AK) **4**, 3613 (AK) **4**, 3772 (AK) **4**, 4037 (AK) **4**; Osborne s.n. (AK, 2 sheets, male) **1**.

Parris & Keen s.n. (AK 110746) **4**; Parsons 225 (CHR) **4**, 226 (CHR) **4**; Petrie in Dec. 1886 (WELT, mixed collection with **5**) **3**, in Dec. 1888 (WELT) **5**, in 1890 (WELT) **5**, in Oct. 1892 (WELT) **3**, in Nov. 1894 (WELT) **4**, in Sep. 1896 (WELT) **4**, in 29 Oct. 1898 (WELT) **4**, in Nov. 1906 (WELT) **4**, in Nov. 1908 (WELT) **3**, s.n. (WELT) **4**; Phillips s.n. (AK) **3**, s.n. (AK) **5**; Poole in 8 Jan. 80 (CHR) **3**; Powell s.n. (AK 40243, 44878) **4**, s.n. (CHR) **5**.

Rattenbury s.n. (AK 169927) **4**; Raven 25097 (CHR) **5**, 25112 (CHR) **5**, 25118 (CHR) **4**, 25121 (CHR, 7 sheets) **3**, 25122 (CHR) **4**, 25123 (CHR, 3 sheets) **3**, 25126–1 (CHR) **3**, 25127 (CHR, 10 sheets) **3**, 25128 (CHR) **4**, 25128–2 (CHR) **4**, 25128–3 (CHR) **4**, 25129 (CHR, 10 sheets) **5**, 25130 (CHR) **4**, 25132 (CHR) **3**, 25134 (CHR, 2 sheets) **4**, 25135 (CHR) **4**, 25136 (CHR) **5**, 25137 (CHR) **5**, 25145 (CHR) **1**, 25147 (CHR) **1**, 25181 (CHR) **4**, 25187 (CHR) **4**, 25192–2 (CHR) **3**, 25192–4 (CHR) **3**, 25193 (CHR, 3 sheets) **5**, 25203 (CHR) **4**, 25206–1 (CHR) **3**, 25212 (CHR, 8 sheets) **3**, 25215 (CHR, 4 sheets) **3**, 25216 (CHR, 4 sheets) **5**, 25219 (CHR) **4**, 25220 (CHR, 4 sheets) **5**, 25222 (CHR) **4**, 25223 (CHR) **5**, 25224 (CHR, 7 sheets) **3**, 25227 (CHR) **5**, 25232 (CHR) **5**, 25238 (CHR) **5**, 25239 (CHR, 10 sheets) **3**, 25271 (CHR) **4**, 25272 (CHR) **5**, 25334 (CHR) **4**, 25337 (CHR) **4**, 25346 (CHR) **3**, 25347 (CHR) **5**, 25353 (CHR) **5**, 25358 (CHR) **4**, 25414 (CHR) **4**,

25420 (CHR) **4**, 25431 (CHR) **4**, 25566 (CHR) **5**, 25567 (CHR, 2 sheets) **3**, 35313 (CHR, 36 sheets) **5**, et al. 25214 (CHR) **4**, in 14 Oct. 1969 (CHR) **5**; Rawlings s.n. (CHR) **1**; Rawson in 2 Oct. 1947 (CHR) **4**, in 20 Jan. 1947 (CHR) **4**, in 1954 (CHR, 4 sheets) **3**; Reynolds 155441 (CHR) **1**; Ritchie in 22 Feb. 1966 (CHR) **4**; Ritchie & Ritchie in 16 Sep. 1968 (CHR) **4**; Robins in Dec. 1970 (CHR) **5**; Robins & Mitchell in 6 Jan. 1969 (CHR) **3**.

Sachet 2352 (MO, US) **2**; Salmon in Dec. 1943 (WELT) **4**; Scofield 13 (AK) **4**; Shakespear s.n. (AK 127539) **4**; Simpson 1365 (CHR) **4**, 5505 (CHR) **4**, 6123 (CHR) **5**, 6124 (CHR) **5**, 6628 (CHR) **5**, 7076 (CHR) **5**, 7459 (CHR) **3**, 8251 (CHR) **3**, in 20 Jan. 1968 (CHR) **5**; Simpson & Chapman 6926 (CHR) **3**; Simpson & Macmillan in 20 Jan 1968 (CHR) **3**; Smith 165 (CHR) **3**, 166 (CHR) **5**, 188 (CHR) **2**, in 8 Feb. 1974 (CHR) **5**, s.n. (AK 118077, 109157) **4**; Smith-Dodsworth s.n. (AK) **1**; St. John & Fosberg 17005 (BISH) **2**; Sykes in 14 Apr. 1971 (CHR) **4**.

Talbot in 1947 (CHR) **3**, in Jan. 1949 (CHR) **3**, s.n. (CHR) **3**; Taylor in 29 Nov. 1970 (CHR) **4**; Thomson 981/ 1 (CHR) **5**; Travers s.n. (K) **3**; Trevarthen s.n. (AK) **1**; Troup s.n. (AK 119584) **4**; Tryon s.n. (AK, mixed with **3**) **5**.

Veillon & Guérin 38 (BISH, P, PAP, US) **2**; Veitch s.n. (CHR 191554) **4**.

Wanganui Museum Botanical Group 40 (CHR) **4**; Wardle in Nov. 1964 (CHR) **5**, in 2 Nov. 1966 (CHR) **4**, in 30 Nov. 1970 (CHR) **4**, in 2 Dec. 1970 (CHR) **5**, in 4 Dec. 1970 (CHR) **3**, in 5 Dec. 1970 (CHR) **3**, in 5 Jan. 1975 (CHR) **3**, in 8 Dec. 1975 (CHR) **3**, in 7 Jan. 1977 (CHR) **4**, in 31 Mar. 1977 (CHR) **3**, in 10 Jan. 1985 (CHR) **5**; Wardle & Fryer in 4 Nov. 1968 (CHR) **3**; Wardle & Myers in 3 Dec. 1969 (CHR) **3**, in 3 Dec. 1969 (CHR) **5**; Wilson 789–559 (CHR) **5**, 789–85 (CHR) **4**; Wood in 7 Jan. 1954 (AK 32524, mixed collection with **5**) **3**, in 29 Nov. 1987 (CHR) **4**, s.n. (AK 27666) **4**, s.n. (AK 118587) **4**; Wright 2226 (AK) **4**, 3505 (AK) **4**, 3687 (AK) **4**, 512 (AK) **4**, 5332 (AK) **1**, 5389 (AK) **1**, 5510 (AK) **1**, 5600 (AK) **1**, 633 (AK) **4**, 7094 (AK) **1**, 781 (AK) **4**.

Yaldwyn in 1 Mar. 1972 (WELT) **4**.

Zotov 193 (CHR) **4**, in 1 Oct. 1929 (CHR) **3**, in 6 Oct. 1929 (CHR) **5**, in 3 Mar. 1962 (CHR, 2 sheets) **4**, in 28 Dec. 1972 (CHR) **3**.